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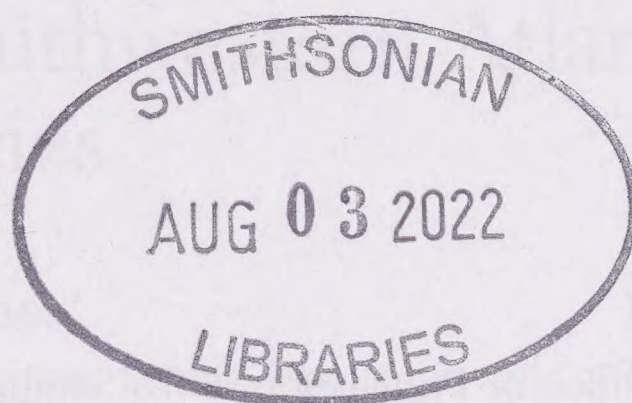
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A new species of *Tritonoharpa* Dall, 1908 (Gastropoda: Cancellariidae) from the southwestern Atlantic and an overview of other western Atlantic species

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ABSTRACT

A new southwestern Atlantic species belonging to genus *Tritonoharpa* is described from northeastern and southeastern Brazil. *Tritonoharpa curvapex* new species has a strongly deviated nucleus in the protoconch, which is the main feature that distinguishes it from the remaining congeners from the western Atlantic. Shell dimensions and number of cords in the teleoconch also distinguish this new species from the other *Tritonoharpa*. An overview of the remaining extant *Tritonoharpa* from the western Atlantic is also presented. We provide taxonomical remarks, illustrations and the known distribution of *Tritonoharpa lanceolata* (Menke, 1828), *Tritonoharpa cubapatriae* (Sarasúa, 1975), *Tritonoharpa bayeri* (Petuch, 1987), *Tritonoharpa leali* Harasewych, Petit, and Verhecken, 1992 and *Tritonoharpa janowskyi* Petuch and Sargent, 2011.

Additional Keywords: Neogastropoda, Volutoidea, Plesiotritoninae, taxonomy

INTRODUCTION

The family Cancellariidae Forbes and Hanley, 1851 consists of marine gastropods and is known from all oceans (Lima et al., 2007), but the majority of the species are tropical or temperate (Harasewych and Petit, 2011). This family currently comprises about 350 extant species (MolluscaBase, 2020) and presents a great variety of shell features (Modica et al., 2011b). Most recent classifications include three subfamilies: Cancellariinae Forbes and Hanley, 1851, Admetinae Troschel, 1865 and Plesiotritoninae Beu and Maxwell, 1987 (Modica et al., 2011b; Bouchet et al., 2017).

Among the Plesiotritoninae, the genus *Tritonoharpa* Dall, 1908 is one of the most diverse with 19 extant valid species (MolluscaBase, 2018). Five species of *Tritonoharpa* are known from the western Atlantic: *T. lanceolata* (Menke, 1828), *T. cubapatriae* (Sarasúa, 1975), *T. bayeri* (Petuch, 1987), *T. leali* Harasewych, Petit and Verhecken,

1992 and *T. janowskyi* Petuch and Sargent, 2011. *Tritonoharpa lanceolata* is currently known from several localities in the western Atlantic, occurring from the eastern USA to southeastern Brazil (Beu and Maxwell, 1987; Rios, 2009). *Tritonoharpa cubapatriae* is known from Cuba and Panama (Caribbean coast) (Sarasúa, 1975; Lee, 2009). *Tritonoharpa bayeri* and *T. janowskyi* are known only from their type localities off Caribbean Colombia and Florida, USA, respectively. *Tritonoharpa leali* is currently restricted to the states of Bahia, Espírito Santo, and Rio de Janeiro, Brazil (Harasewych et al., 1992; Absalão et al., 2006). Thus, until now *T. lanceolata* and *T. leali* are the only species recorded in Brazil (Harasewych et al., 1992; Absalão et al., 2006; Rios, 2009).

Verhecken (1991) commented on the scarcity of records or descriptions of Cancellariidae in the western Atlantic south of the Equator, but since then reports on cancellariids from Brazil increased considerably, especially in deep-sea studies (Harasewych et al., 1992; Simone and Birman, 2006; Barros and Lima, 2007; Barros and Petit, 2007; Lima et al., 2007). Recent surveys of malacological collections in Brazil revealed an undescribed species of *Tritonoharpa* from the coast of Brazil and the need for a revision of other known congeners in the western Atlantic. We formally describe *Tritonoharpa curvapex* new species and provide taxonomical comments on the other western Atlantic *Tritonoharpa*.

MATERIALS AND METHODS

The material studied consists mostly of empty shells deposited in malacological collections, collected by various oceanographic expeditions and smaller collecting events. The largest expeditions are: 1. REVIZEE Central: “Programa de Avaliação do Potencial Sustentável de Recursos Vivos da Zona Econômica Exclusiva, Score Central” (Program of Evaluation of the Sustainable

Potential of Living Resources in the Economic Exclusive Zone), carried out by “Ministério do Meio Ambiente”, Brazilian government, samples collected by the research vessel (R/V) ANTARES and the supply-boat ASTRO GAROUPA between 1996–2002; 2. BPOT MR: “Projeto de Caracterização e Monitoramento Ambiental da Bacia Potiguar – Malha Regional” (Project of Environmental Characterization and Monitoring of Potiguar Basin – Regional Grid), carried out by Petrobras SA, samples collected by the supply-boat ASTRO GAROUPA between 2002–2004; 3. AMBES: “Caracterização Ambiental Marinha da Bacia do Espírito Santo e porção Norte da Bacia de Campos” (Marine environmental characterization of the Espírito Santo Basin and North part of Campos Basin), carried out by Petrobras SA, samples collected by the R/V LUKE THOMAS and R/V SEWARD JOHNSON, between 2010–2013.

Most shells were photographed (using focus stacking) by an AxioCam ICc 5 camera coupled to a stereomicroscope ZEISS Discovery.V20. A few shells were studied under a scanning electron microscope (SEM) Jeol JSM-6390LV for a detailed examination of sculpture. Shell measurements are: shell length (SL), body whorl length (BWL), aperture length (AL), shell width (SW), aperture width (AW), protoconch height (PCH) and width (PCW). The counting of protoconch whorls follows Verduin (1982) and Verhecken (2007). Some shells were treated with mineral oil to enhance the color pattern.

Collection acronyms are: ANSP: Academy of Natural Sciences of Philadelphia, Drexel University, Philadelphia; FLMNH: Florida Museum of Natural History, Gainesville; IBUFRJ: Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MNRJ: Museu Nacional, Rio de Janeiro, Brazil; MORG: Museu Oceanográfico “Professor Eliézer de Carvalho Rios”, Universidade Federal do Rio Grande, Rio Grande, Brazil; MZSP: Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; SMF: Naturmuseum Senckenberg, Frankfurt, Germany; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC.

Due to the recent fire at the Museu Nacional in Brazil (Zamudio et al., 2018) most lots from this institution listed in the material examined here, in addition to lots lent from other institutions, were destroyed. Destroyed specimens (spm) or shells (sh) are marked by a dagger (†) in the material examined of each species.

SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Subfamily Plesiotritoninae Beu and Maxwell, 1987

Genus *Tritonoharpa* Dall, 1908

Nivitreron Iredale, 1929. Type species: *Triton antiquatus* Hinds in Reeve, 1844 (by original designation); Recent, tropical Indo-Pacific.

Esbelta Sarasúa, 1975. Type species: *Ranella lanceolata* Menke, 1828 (by original designation); Miocene to Recent, western Atlantic.

Type Species: *Tritonoharpa vexillata* Dall, 1908 (by original designation); Recent, western America and the Galapagos Island.

Description: Shell with weakly to moderately convex teleoconch whorls, retaining prominent varices on early as well as later whorls, well developed columellar collar, lacking columellar plaits or with a single very low, narrow columellar plait, and with a nematoglossan radula, consisting of a thin membrane and one central row of rachidian teeth (adapted from Beu and Maxwell, 1987 and Modica et al., 2009).

Tritonoharpa curvapex new species (Figures 1–9)

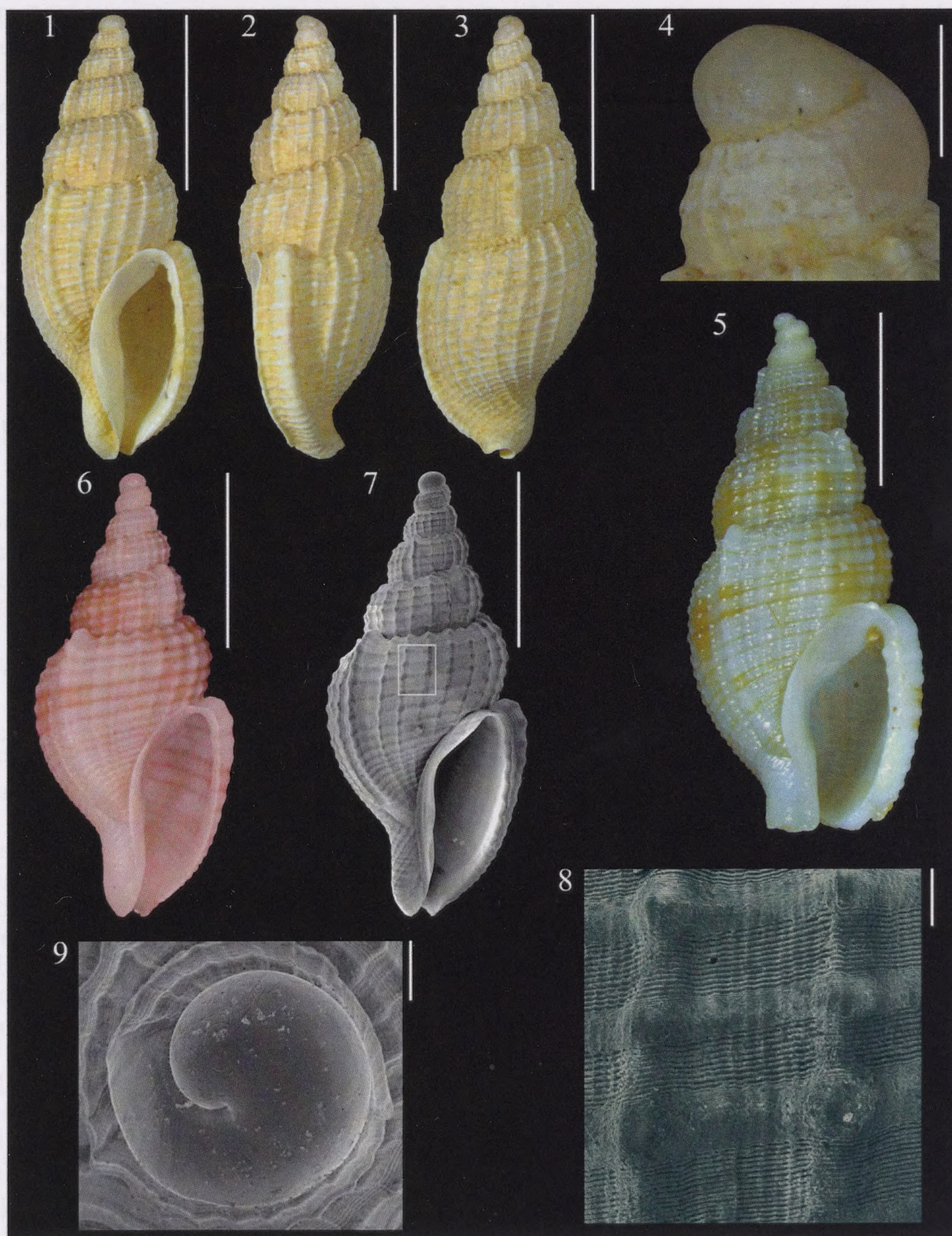
Diagnosis: Shell up to 15.0 mm long, 5.5 mm wide, with 6–7 whorls, cream to light brown, with scattered brown blotches and thin spiral bands. Whorls convex, with moderately prominent varices (1–2 per whorl) from early whorls to later whorls, sculptured with cancellate pattern. Protoconch paucispiral, smooth, 1.0 whorl, nucleus strongly deviated.

Description: Shell about 15.0 mm long, 6.5 mm wide, spire angle 35°, shouldered. Protoconch paucispiral, 1.0 whorl, nucleus deviated about 30° from teleoconch axis. Protoconch–teleoconch transition abrupt, marked by a thin lip and onset of cancellate sculpture. Teleoconch with up to 7 whorls, moderately inflated, weakly shouldered; suture deeply impressed, almost obscured by the axial coronation of succeeding whorl. Spiral and axial cords present, producing cancellate sculpture; strong nodules at the intersection of spiral and axial cords; spiral cords more pronounced than axial cords. Varices high, non-collabral, narrow, appearing periodically in every 2/3 whorl. About 11 axial ribs between varices in the last whorl; About 16 spiral cords from the suture to the beginning of the siphonal canal in the last whorl (frontal view). Aperture wide, elliptical, with well-defined posterior notch. Inner lip smooth, with columellar collar reflected over, but not adherent to, fasciole and pseudoumbilicus. Outer lip with up to 8 pairs of denticles confined to flared region beyond varix. Siphonal canal short, weakly deviated, partially covered abaxially. Shell color cream to brownish, with scattered brownish blotches and thin spiral bands.

Type Locality: Brazil: Northeast coast, imprecise locality between Pernambuco and Bahia states, coll. 1977.

Type Material: Holotype: IBUFRJ 5430 (sh). **Paratypes:** Brazil: Bahia state: Camamu Basin, 13°28'29" S 38°48'41" W, 30 m (MNRJ 14925, 1 sh†; MNRJ 27973, 1 sh†); Espírito Santo state: REVIZEE Central I stn. C65, 18°52'58" S 39°06'00" W, 50 m, coll. R/V Antares, 25/iv/1996 (IBUFRJ 9525, 1 sh).

Measurements: Holotype, IBUFRJ 5430: Whorls = 6.0; SL = 12.7 mm; BWL = 8.5 mm; AL = 6.0 mm; SW = 5.2 mm; AW = 2.7 mm; PCH = 0.8 mm; PCW = 0.9 mm; SL/SW = 2.4.



Figures 1–9. *Tritonoharpa curvapex* new species. 1–4. Holotype, IBUFRJ 5430. 5. Paratype, MNRJ 27973. 6–9. Paratype, MNRJ 14925. 1, 5–7. Entire shell in frontal view, white square in 7 indicates detail in 8. 2. Entire shell in lateral view. 3. Entire shell in dorsal view. 4, 9. Detail of protoconch, lateral and apical views, respectively. 8. Detail of teleoconch surface. Scale bars: 1–3, 5–7 = 5 mm; 4 = 500 μm ; 8–9 = 200 μm .

Etymology: *Curvus*, Latin for bent; *apex*, Latin for tip; referring to the strongly deviated nucleus of the protoconch.

Distribution: Brazil: From Pernambuco to Espírito Santo. Empty shells from depths between 30 m to 50 m.

Remarks: The holotype IBUFRJ 5430 (Figures 1–4) and the paratype IBUFRJ 9525 of *T. curvapex* are safely preserved in the IBUFRJ collection. The other paratypes (Figures 6–9) were destroyed by the fire. To avoid the

designation of a destroyed specimen as the holotype, the shell of IBUFRJ 5430 was selected as the holotype despite the imprecise locality of collection.

Tritonoharpa curvapex differs from all other western Atlantic species of the genus in having a conspicuous protoconch in which the nucleus is strongly deviated (Figures 4, 9). This newly described species is most similar to *T. bayeri* (Figures 23–27) based on the general shape and on having an aperture that is not very constricted posteriorly. The protoconch of the holotype of *T. bayeri* (USNM

859853) is partially broken (Figures 25, 26), but it is possible to note that the nucleus is not deviated as in *T. curvapex*. *Tritonoharpa curvapex* can also be distinguished from *T. bayeri* by the relatively smaller dimensions of the shell (12.7 mm long, 5.2 mm wide *vs.* 16.2 mm long, 7.6 mm wide, respectively, both with 5 whorls) and by the smaller number of axial ribs between varices of the last whorl (11 *vs.* 16–18). These species also differ by their color pattern, *T. curvapex* has brownish spots like *T. bayeri*, but also some spiral bands (Figure 5) that are not present in *T. bayeri*.

Tritonoharpa curvapex also resembles *Tritonoharpa ponderi* Beu and Maxwell, 1987, from Australia, and *Tritonoharpa caunbonensis* Pacaud, Ledon, and Loubry, 2015, an extinct species from the Eocene of Paris Basin, because these species also have a strongly deviated protoconch (Beu and Maxwell, 1987: pl. 18, fig. E, I; Pacaud et al., 2015: pl. 10, fig. 1E). However, *T. curvapex* can be distinguished from *T. ponderi* by the abrupt increase in diameter of the teleoconch, which occurs more gradually in *T. ponderi*. *Tritonoharpa curvapex* can be distinguished from *T. caunbonensis* by its relatively larger size (holotype of *T. curvapex*, IBUFRJ 5430, ~6 whorls, 12.7 mm long, 5.2 mm wide, SL/SW = 2.4 *vs.* holotype of *T. caunbonensis*, MNHN.F.A51472, ~7 whorls, 10 mm long, 3.9 mm wide, SL/SW = 2.6), and in having thinner varices and a narrower inner lip.

Notes on Other Western Atlantic *Tritonoharpa*

Tritonoharpa lanceolata (Menke, 1828)

(Figures 10–20)

Ranella lanceolata Menke, 1828: 87.

For synonymy up to 1987, see Beu and Maxwell (1987: 40) *Colubraria lanceolata* (Menke, 1828) – Perry and Schwengel (1955: 158, pl. 31, fig. 222); Daccarett and Bossio (2011: 94, fig. 444).

Tritonoharpa lanceolata (Menke, 1828) – Lyons (1989: 26, pl. 9, fig. 1); Lyons (1998: 27 [annotated list]); Petit and Harasewych (2005: 63 [annotated list]); Wolfe (2008 [annotated list]); Tunnell Jr. et al. (2010: 234); Espinosa et al. (2012: 291, fig. 525); Lamy and Pointier (2017: 528, pl. 184, fig. 9A–B).

Type Locality: Puerto Rico (Menke, 1828).

Type Material: Probably lost. After K.T. Menke's death his collection was sold and dispersed (Zilch, 1967; Kohn, 1988). The most probable place to find would be the SMF, however there is no material that seems to belong to Menke's material of *T. lanceolata* (Sigrid Hof, pers. comm.).

Other Material Examined: USA: Georgia: off Georgia (30°54'18" N, 80°36'06" W, 34 m), coll. R/V BAGBY, 26/iii/1980: USNM 824010 [3 sh]; Florida: 12 miles Northeast Cape Canaveral (28°37' N, 80°30' W): USNM 486176 [1 sh]; Oculina Reef (27°50' N, 79°58' W, 91 m), coll. Houbrick: USNM 798073 [1 sh]; W of Boca Grande (26°44' N, 84°09' W, 55 m), coll. 1971: ANSP 395042 [6

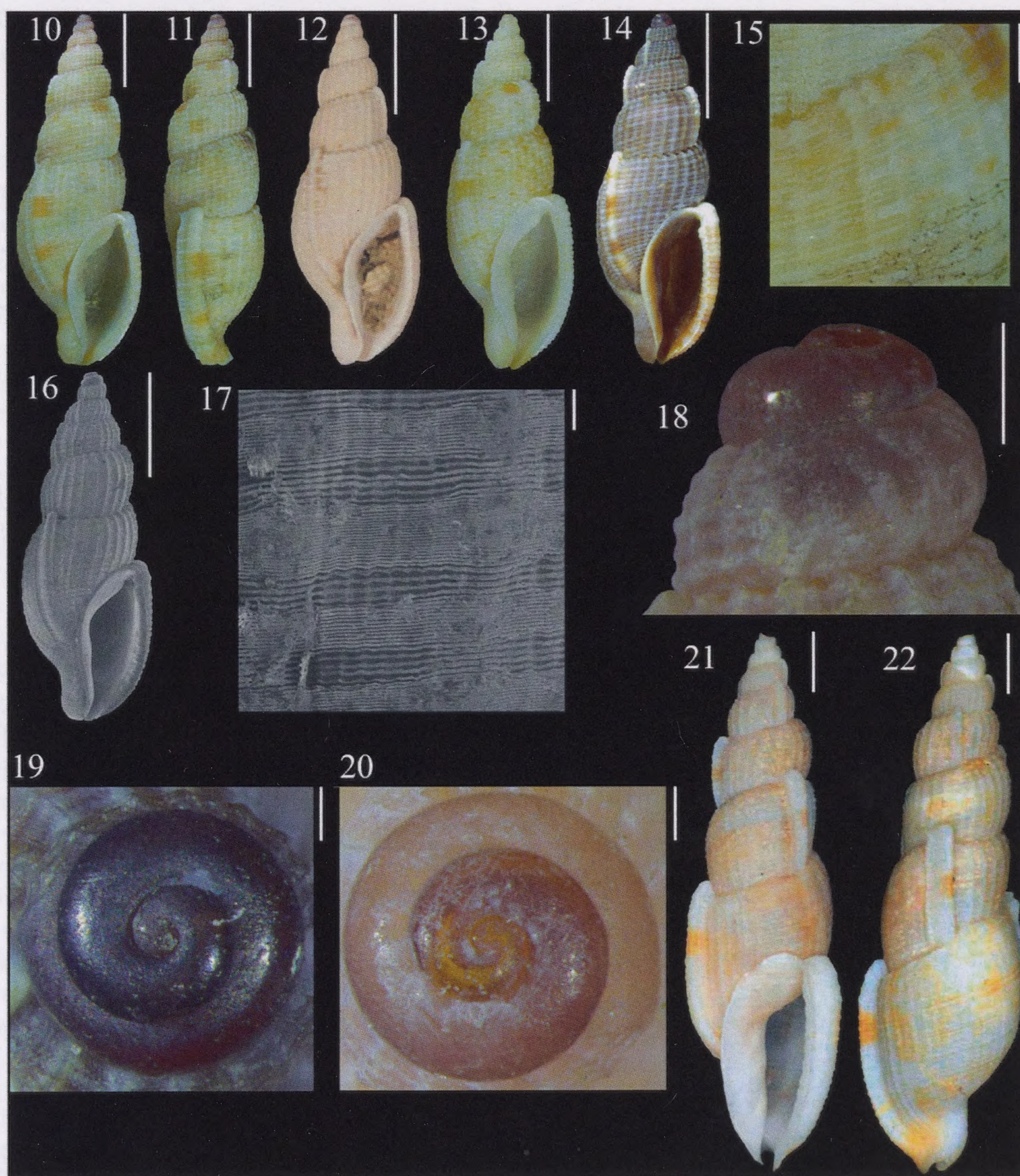
sh]; Off Key West (182–213 m), coll. IX/1963: ANSP 294763 [1 sh]. Caribbean area: Jamaica: Montego Bay, coll. A. L. Mhering, 17/xii/1954: USNM 712137 [1 sh]. Panama: Minas Bay, Payardi Island: USNM 743644 [2 sh]. Haiti: Jeremy: USNM 383239 [1 sh]. Dominican Republic: Las Galeras, Samaná Bay (2 m), coll. 1994: ANSP 408384 [2 sh]. Puerto Rico: North of Mayaguez Docks: USNM 662026 [2 sh]. Virgin Islands: St. Thomas, coll. Brady, 1968: USNM 702792 [2 sh]. Anguilla: Sombrero Island: USNM 92993 [1 sh]. Grenada: Grand Anse Bay (12°01'46" N, 61°46'19" W, 3–6 m), coll. 08/x/2012: MZSP 108664 [1 sh]. Trinidad and Tobago: Off Scarborough, coll. 30/xi/1989: FLMNH 281379 [7 sh†].

Measurements: USNM 92993: Whorls = 8.0; ANSP 395042: SL = 29.1 mm; BWL = 17.0 mm; AL = 11.5 mm; SW = 9.0 mm; AW = 6.0 mm; PCH = not measured; PCW = not measured; SL/SW = 3.2. Whorls = 7.5; SL = 24.1 mm; BWL = 14.3 mm; AL = 10.1 mm; SW = 8.6 mm; AW = 4.8 mm; PCH = 1.1 mm; PCW = 1.2 mm; SL/SW = 2.8. ANSP 294763: Whorls = 7.0; SL = 20.2 mm; BWL = 13.7 mm; AL = 9.7 mm; SW = 7.0 mm; AW = 4.4 mm; PCH = 0.8 mm; PCW = 1.0 mm; SL/SW = 2.9.

Distribution: USA: New Jersey, North Carolina, Georgia, Florida (Beu and Maxwell 1987), Texas (Rosenberg et al., 2009; Tunnell Jr. et al., 2010). Bermuda (Lamy and Pointier, 2017); Bahamas (Beu and Maxwell, 1987; Redfern, 2013); Cuba; Haiti (Beu and Maxwell, 1987); Mexico (Vokes and Vokes, 1983; Beu and Maxwell, 1987); Jamaica (Beu and Maxwell, 1987); Honduras (Lamy and Pointier, 2017); Costa Rica (Lamy and Pointier, 2017); Panama (Lamy and Pointier, 2017); Colombia (Daccarett and Bossio, 2011); Puerto Rico (Menke, 1828); Virgin Islands (Mörch, 1877; Beu and Maxwell, 1987); St. Martin (Lamy and Pointier, 2017); Anguilla (Lamy and Pointier, 2017); Guadeloupe (Mörch, 1877; Lamy and Pointier, 2017); Martinique (Mörch, 1877); Trinidad and Tobago (Beu and Maxwell, 1987); Venezuela (Beu and Maxwell, 1987); Suriname (Altena, 1975); Brazil: from North to Southeast coast (?) (Rios 2009). From 0 to 178 m (Rosenberg et al., 2009).

Remarks: The whereabouts of the type material of *T. lanceolata* is unknown and as mentioned above, it is probably lost. The original description is not very informative and the species was not figured by Menke (1828), consequently the true identity of *T. lanceolata* is challenging to assess despite being frequently cited in the literature. We have examined one shell from Puerto Rico, area of the type locality which was not precisely defined, but this specimen is severely worn (Figure 12). We follow here the description of Beu and Maxwell (1987) and Harasewych et al. (1992) to recognize *T. lanceolata*.

Tritonoharpa lanceolata usually has slightly distorted teleoconch whorls (Figures 10–14, 16) in comparison to its congeners and reaches a larger size. Beu and Maxwell (1987) described a variation of the teleoconch sculpture in *T. lanceolata*, in which axial and spiral cords vary from narrow to thick, resulting in different degrees of



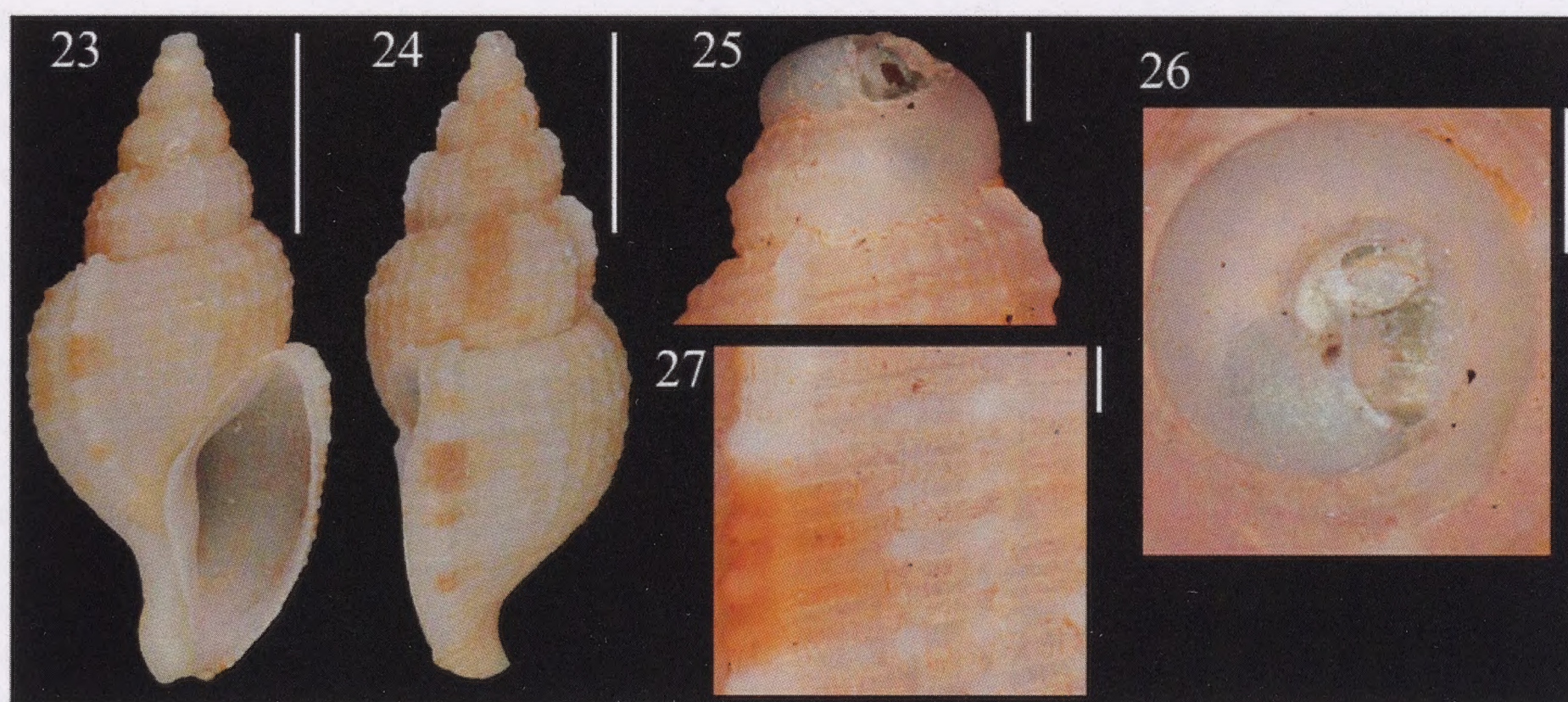
Figures 10–22. *Tritonoharpa* species. **10–20.** *Tritonoharpa lanceolata* (Menke, 1828). **10, 11, 18, 20.** ANSP 395042. **12.** USNM 662026. **13, 15.** ANSP 294763. **14, 16, 17, 19.** ANSP 408384. **21, 22.** *Tritonoharpa cubapatriae* (Sarasúa, 1975): holotype, Museo Poey, Universidad de La Habana, Cuba. **10, 12–14, 16, 21.** Entire shell in frontal view. **11.** Entire shell in lateral view. **15, 17.** Detail of teleoconch sculpture. **18.** Detail of protoconch in lateral view. **19, 20.** Detail of protoconch in apical view. **22.** Entire shell in dorsal view. Scale bars: **10–14, 16, 21, 22** = 5 mm; **15** = 1 mm; **17** = 100 μ m; **18** = 500 μ m; **19, 20** = 200 μ m. Credits: **19, 20,** José Espinosa.

nodulation. Harasewych et al. (1992: 45, fig. 8) depicted a detail of the sculpture of *T. lanceolata*, showing spiral cords more pronounced and thicker than axial cords. Shells of *T. lanceolata* examined here also show well developed spiral cords and weaker axial cords (Figure 17).

Tritonoharpa lanceolata also has a variable color pattern in the protoconch and teleoconch (Beu and Maxwell, 1987). As currently known, the protoconch varies from pale cream (Figures 12, 13) to purplish (Figures 10, 14, 18–20) and the teleoconch varies from homogeneous pale cream with brownish spots and streaks (Figures 10, 13) to darker shells (Figure 14). Whitish shells are usually beach worn specimens (Figure 12). Until more

evidence about the identity of *T. lanceolata* become available (i.e., discovery of the type material, anatomy, genetics, more material from Puerto Rico), it is difficult to assess if there is more than one distinct species under the same name.

In Brazil, the first record of *T. lanceolata* was reported by Rios (1970) (as “*Colubraria lanceolata*”), who cited localities from the Northeast and Southeast (Trindade Island) regions. Rios (1975; 1985) added a record from the North of Brazil. Later, Rios (1994) recorded *T. lanceolata* only in Pará, North Brazil and Rios (2009) repeated again the records from North to Southeast coast of Brazil. Rios’ illustrations (1975; 1985; 1994;



Figures 23–27. *Tritonoharpa bayeri* (Petuch, 1987): holotype of *Colubraria bayeri* Petuch, 1987, USNM 859853. **23.** Entire shell in frontal view. **24.** Entire shell in lateral view. **25, 26.** Detail of protoconch in lateral and apical views, respectively. **27.** Detail of teleoconch sculpture. Scale bars: **23, 24** = 5 mm; **25–27** = 400 μ m. Credits: **23, 24**, USNM.

2009) do not permit the evaluation of the pattern of sculpture in the teleoconch. Thus, a robust delimitation of the species based on these figures is not possible. Furthermore, despite being a catalogue of mollusks from Brazil, the shells figured by Rios are not always from this country (pers. obs.).

The malacological collections studied in the present work usually housed vouchers from Brazil identified as *T. lanceolata*. However, all the shells from Brazil studied seems to present axial ribs thicker and slightly more pronounced in comparison to the material from the northern hemisphere, but a few shells were studied under SEM. These features lead us to doubt whether *T. lanceolata* does really occur in Brazil.

***Tritonoharpa cubapatriae* (Sarasúa, 1975)**
(Figures 21, 22)

Colubraria (*Esbelta*) *cubapatriae* Sarasúa, 1975: 4, figs. 1–2. *Tritonoharpa cubapatriae* (Sarasúa, 1975) – Petit and Harasewych (1990: 17 [annotated list]; 2005: 42 [annotated list]); Lee (2009: 123); Rosenberg et al. (2009: 661 [annotated list]); Espinosa et al. (2012: 291, fig. 524 [reproduced from original illustration]).

Type Locality: Cuba: Habana: Marianao, 20 m.

Type Material: Holotype: Museo Poey, Universidad de La Habana, Cuba (sh; here examined). Formerly at “Instituto de Zoología, Academia de Ciencias de Cuba” and catalogued as type number 31 (sh; here examined by photographs) (Sarasúa 1975).

Distribution: Cuba (Sarasúa, 1975); Panama (Lee, 2009). Known from 20 m (Sarasúa, 1975).

Remarks: Beu and Maxwell (1987: 39) considered this species as the possible largest specimen of *T. lanceolata*

due to the size of the holotype (45 mm long) (Sarasúa, 1975) (Figures 21, 22). According to these authors: “examination of more extremely large western Atlantic specimens will be necessary to be sure of the status of *T. cubapatriae*”. Indeed, the differences pointed by Sarasúa (1975) in comparisons with *T. lanceolata* may be related to the ontogeny phase of the species and we agree with Beu and Maxwell (1987) in that the shell of *T. cubapatriae* does not have more convex whorls than *T. lanceolata*.

The largest specimen of *T. lanceolata* we have examined reaches about eight whorls, 29.1 mm long, collected in Anguilla, Caribbean (USNM 92993). Lamy and Pointier (2017: pl. 184, figs. 9A, B) illustrated a shell from Martinique with 38.4 mm long.

The only additional record of *T. cubapatriae* since its original description was reported by Lee (2009: 123). He referred to material from Caribbean Panama in a private collection, with no information about depth and no illustration.

***Tritonoharpa bayeri* (Petuch, 1987)**
(Figures 23–27)

Colubraria bayeri Petuch, 1987: 102, pl. 24, figs. 11–12. *Colubraria bayeri* Petuch, 1987 – Daccarett and Bossio (2011: 94, fig. 446).

Tritonoharpa bayeri (Petuch, 1987) – Lamy and Pointier (2017: 528, pl. 184, fig. 8A–B).

Type Locality: Colombia: Guajira Peninsula, Off Cabo La Vela, 35 m.

Type Material: Holotype: USNM 859853 (sh; here examined).

Measurements: Holotype, USNM 859853: Whorls = 7.0; SL = 16.2 mm; BWL = 11.5 mm; AL = 8.3 mm; SW = 7.6 mm; AW = 3.7 mm; PCH = 1.0 mm; PCW = 1.2 mm; SL/SW = 2.1.

Distribution: Guadeloupe (Lamy and Pointier, 2017), Colombia (Petuch, 1987; Daccarett and Bossio, 2011). From 8 to 35 m (Petuch, 1987; Lamy and Pointier, 2017).

Remarks: *Tritonoharpa bayeri* was known only from Colombia until recently when Lamy and Pointier (2017) recorded the species in Guadeloupe. The shell figured by Lamy and Pointier (2017: pl. 184, fig. 8A–B) has a dark brown coloration at the spire, differing from the holotype.

Petuch (1987) introduced the species in *Colubraria* Schumacher, 1817 and made no comparisons to other species of *Tritonoharpa*. *Tritonoharpa bayeri* is very similar to *T. curvape* and was distinguished above.

Tritonoharpa bayeri differs from *T. lanceolata* and *T. leali* by the faster increase in diameter, reaching a smaller ratio of the SL/SW (2.1 vs. 2.8–3.2 and 2.6, respectively). Furthermore, the aperture of *T. bayeri* is not so constricted posteriorly as in *T. lanceolata* and *T. leali*.

Tritonoharpa bayeri has a similar ratio of SL/SW to the initial whorls of *T. cubapatriae*, the latter species cease a strong increase in diameter after the fifth or sixth whorl and becomes more cylindrical in shape, reaching a higher number of whorls and length. The presence of thinner and lower varices in *T. bayeri* through all whorls indicates that this species is not a young specimen of *T. cubapatriae*.

***Tritonoharpa leali* Harasewych, Petit, and Verheeken, 1992**

(Figures 28–39)

Tritonoharpa leali Harasewych, Petit and Verheeken, 1992: 45, figures 1–2, 5–6.

Tritonoharpa leali Harasewych, Petit and Verheeken, 1992 – Rios (1994: 155, pl. 51, fig. 683A); Absalão et al. (2006: 244); Rios (2009: 298, fig. 750).

Type Locality: Brazil: Vitória-Trindade Seamount Chain, Davis Bank, MD55 stn. DC40, 20°40' S, 34°41' W, 60 m, coll. R/V MARION DUFRESNE, v/1987.

Type Material: **Holotype:** MORG 28659 (sh; here examined). **Paratype:** Brazil: Bahia state: off Itaparica Island (USNM 860521, 1 sh; here examined).

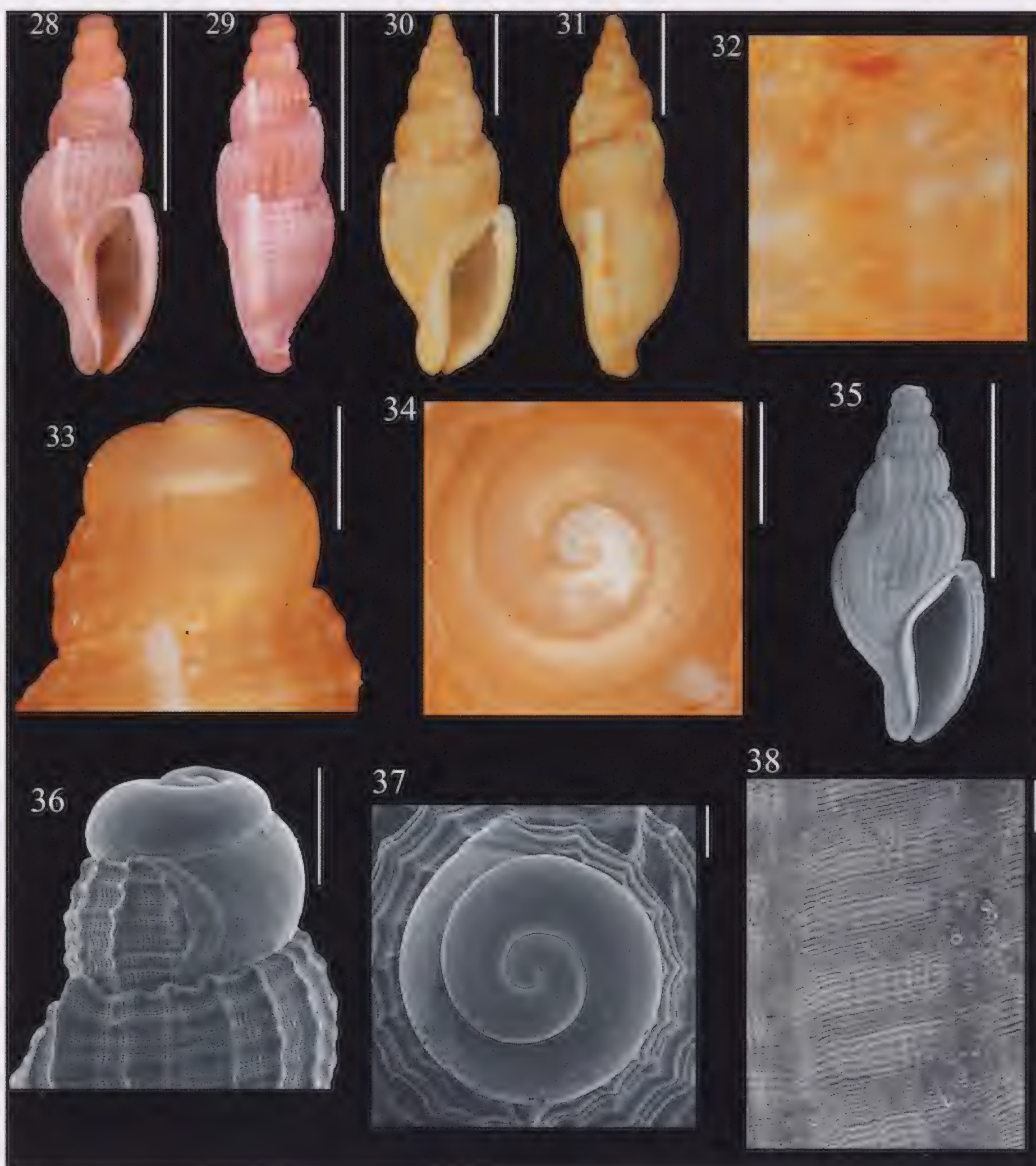
Other Material examined: Brazil: Rio Grande do Norte state: BPOT stn. MR45 (04°27'18" S, 37°04'41" W, 47 m), coll. 01/v/2010: MNRJ 34461 [2 sh†]; BPOT stn. MR41 (04°49'39" S, 36°10'08" W, 59 m), coll. 27/x/2009: MNRJ 34462 [1 sh†]; Bahia state: Salvador, Barra (10–15 m), coll. B. Linhares, xii/1992: MNRJ 21547 [6 sh†]; (13°19'52" S, 38°52'52" W, 33 m): MNRJ 27933 [1 sh†]; (13°27'58" S, 38°44'38.40" W): MNRJ 28108 [1 sh†]; (13°27'58" S, 38°46'26.40" W, 35 m): MNRJ 14931 [1 sh†]; (13°28'01.20" S, 38°48'00" W, 30 m): MNRJ 14926 [1 sh†]; (13°28'30" S, 38°48'43.20" W, 30 m): MNRJ 14927 [1 sh†]; (13°29'42" S, 38°48'18" W, 33 m): MNRJ 14928

[1 sh†], MNRJ 34464 [1 sh†]; (13°30'43" S, 38°49'08.40" W, 29 m): MNRJ 28848 [1 sh†]; REVIZEE Central V stn. 5R (15°34'05" S, 38°49'48" W, 20 m), coll. 25/x/1997: IBUFRJ 12282 [1 sh†]; REVIZEE Central I stn. C76 (15°53'49" S, 38°31'05" W, 66 m), coll. 30/iv/1996: IBUFRJ 9186 [1 sh]; IBUFRJ 10115 [1 sh]; Off Nova Viçosa, Abrolhos reef (17°57'58" S, 38°42'18" W), coll. P. Young and C. B. Castro, 19/iii/1993: MNRJ 10167 [1 spm†]; REVIZEE Central V stn. 16R (18°03'32" S, 37°18'54" W, 100 m), coll. 29/vi/2001: IBUFRJ 14437 [1 sh]; REVIZEE Central I stn. C66 (18°19'59" S, 38°55'01" W, 41 m), coll. 26/iv/1996: IBUFRJ 9069 [1 sh]; Espírito Santo state: REVIZEE Central I stn. VV38 (19°28'26" S, 38°22'30" W, 71 m), coll. 29/ii/1996: IBUFRJ 9809 [1 sh]; REVIZEE Central I stn. D39 (19°28'41" S, 38°22'26" W, 84 m), coll. 29/ii/1996: IBUFRJ 7755 [1 sh]; REVIZEE Central I stn. VV24 (20°00'18" S, 39°54'36" W, 45 m), coll. 27/ii/1996: IBUFRJ 13027 [1 sh]; REVIZEE Central VI stn. Y7 (20°50'56" S, 40°10'01" W, 75 m), coll. 28/vi/2002: IBUFRJ 16324 [1 sh]; REVIZEE Central II stn. 35R (20°52'01" S, 40°10'01" W, 55 m), coll. 03/xi/1997: IBUFRJ 12367 [1 sh]; AMBES 7 stn. A2 (21°03'29" S, 40°22'59" W, 40 m): MNRJ 34945 [1 spm†]; Rio de Janeiro state: Arraial do Cabo, Forno beach: (22°57'58" S, 42°00'54" W), coll. M.R. Sá and G. Nunan, 18/xii/1983: MNRJ 14521 [1 sh†]; Arraial do Cabo, Prainha beach, coll. P.M.S. Costa: MNRJ 22245 [1 sh†]; (22°57'58" S, 42°00'39" W, 6 m), coll. 18/iii/2005: MZSP 49326 [1 sh]; São Paulo state: Ilhabela, Vitória Island (~23°44'59" S, 45°01'00" W, 3–10 m), coll. 06/xii/2012: MZSP 109352 [3 spm].

Measurements: Holotype, MORG 28659: Whorls = 5.5; SL = 9.2 mm; BWL = 6.2 mm; AL = 4.4 mm; SW = 3.6 mm; AW = 2.1 mm; PCH = not measured; PCW = not measured; SL/SW = 2.6; Paratype USNM 860521: Whorls = 7.0; SL = 18.0 mm; BWL = 12.0 mm; AL = 7.8 mm; SW = 6.9 mm; AW = 4.0 mm; PCH = 0.9 mm; PCW = 1.0; SL/SW = 2.6.

Distribution: Brazil: Rio Grande do Norte (present study); Bahia (Harasewych et al., 1992; this study); Vitória-Trindade Seamount Chain (Harasewych et al., 1992); Rio de Janeiro (present study); São Paulo (present study). From 3 m to 100 m.

Remarks: Harasewych et al. (1992) pointed out some differences between *T. leali* and *T. lanceolata*, mentioning a “more inflated and thinner shell” in the former. The holotype of *T. leali* (Figures 28, 29) is a relatively young individual, with a stocky appearance, however the species reaches a larger size (MNRJ 21548: one shell reaching 21.2 mm long) and in this case the general shape becomes more elongated and more similar to the shape of *T. lanceolata*. Small specimens of *T. lanceolata* also have a more inflated appearance as noted by Beu and Maxwell (1987: 40). Another difference pointed by Harasewych et al. (1992) was the presence of axial cords more pronounced than the spiral cords in contrast to *T. lanceolata*. All the shells of *Tritonoharpa* from Brazil examined in the



Figures 28–34. *Tritonoharpa leali* Harasewych, Petit and Verhecken, 1992. **28, 29.** Holotype, MORG 28659; **30–34.** Paratype, USNM 860521. **35, 38.** MNRJ 34462. **36, 37.** MNRJ 34461. **28, 30, 35.** Entire shell in frontal view. **29, 31.** Entire shell in lateral view. **32, 38.** Detail of teleoconch sculpture. **33, 36.** Detail of protoconch in lateral view. **34, 37.** Detail of protoconch in apical view. Scale bars: **28–31, 35** = 5 mm; **32, 33** = 500 μ m; **38** = 100 μ m.

present study, except for the newly described species, are more similar to the pattern of sculpture described by Harasewych et al. (1992) for *T. leali*, despite being slightly thinner (Figure 38) than in the holotype (Harasewych et al., 1992: fig. 6). Thus, the occurrence of *T. lanceolata* in Brazil is considered dubious and previous records are probably misidentifications of *T. leali*.

Tritonoharpa leali was known from the central coast of Brazil from Bahia to Espírito Santo states, and also at the Vitória-Trindade seamount chain (Leal, 1991; Harasewych et al., 1992; Absalão et al., 2006; Rios, 2009). In the present study, the geographic distribution of *T. leali* is extended northwards to the state of Rio Grande do Norte ($\sim 04^{\circ}$ S) and southwards to the state of São Paulo ($\sim 23^{\circ}$ S), both in Brazil.

One live specimen photographed at Arraial do Cabo, Rio de Janeiro, Brazil, and here identified as *T. leali* is

densely spotted of orange in the head-foot area and the tentacles are almost completely orange (Figure 39). This color pattern was also described by Modica et al. (2009) for a shell identified as “*T. antiquata* (Hinds, 1844)” but it actually belongs to a species complex of *T. angasi* (Brazier, 1877) (Modica et al., 2011a: 121, 2011b: 692). The head-foot of specimens identified as *T. lanceolata* from Guadeloupe, illustrated by Lamy and Pointier (2017: 528, text-fig), and from areas near Peanut Island, Florida, figured at the website of Bill Frank (www.jaxshells.org/tlance5.htm), also have a very similar color pattern. This color pattern seems common in the genus. It is also possible to observe a large and flattened penis in the Brazilian specimen (Figure 39), similar to the penis of “*T. antiquata*” (Modica et al., 2009: fig. 7P). A more detailed comparison of the penial morphology is limited by the condition of each specimen (alive *vs.* preserved).



Figure 39. *Tritonoharpa leali* Harasewych, Petit and Verhecken, 1992: live specimen photographed at Prainha, Arraial do Cabo, RJ, Brazil (Photo by P.M.S. Costa), observed under a rock. Black arrow indicates the penis.

***Tritonoharpa janowskyi* Petuch and Sargent, 2011**
(Figures 40–44)

Tritonoharpa janowskyi Petuch and Sargent, 2011: 177, pl. 5, fig. D.

Tritonoharpa janowskyi Petuch and Sargent, 2011 – Petuch (2013: 42, fig. 3.7F [reproduced from original illustration])

Type Locality: USA: Florida: Palm Beach County, Off Palm Beach Island, 120 m.

Type Material: Holotype: USNM 1152535 (sh; here examined).

Measurements: Holotype, USNM 1152335: Whorls= 7.5; SL= 16.0 mm; BWL= 11.0 mm; AL= 8.0; SW= 7.3 mm; AW= 4.0 mm; PCH= 1.1 mm; PCW= 1.1 mm; SL/SW= 2.2.

Distribution: Only known from the type locality.

Remarks: Petuch and Sargent (2011) referred exclusively to the holotype (Figures 40–44) and just a “few other specimens” from the type locality. No other additional record of the species was reported.

Tritonoharpa janowskyi is similar in shape to *T. bayeri* (Figures 23–27), as both have a stocky appearance. The former can be distinguished from *T. bayeri* by the proportionally smaller length and width of the teleoconch, by the thicker varices and by the higher number of axial cords between varices (30 vs. 16–18) (Petuch, 1987; Petuch and Sargent, 2011). *Tritonoharpa janowskyi* has a violet color in the protoconch (Figures 42, 43) while *T. bayeri* has a colorless protoconch (Figures 25, 26), but this difference may be due to the conservation status of the shells. The teleoconch of both species has a similar color pattern of irregular brownish patches (Figures 23, 24, 27, 40, 41, 44).

Tritonoharpa janowskyi differs from *T. leali* in having proportionally bigger dimensions comparing the holotypes of both species. Furthermore, the spiral cords are

more pronounced than axial cords in *T. janowskyi* in contrast to *T. leali*, and the former reaches a higher number of axial cords between varices (30 vs. 22).

DISCUSSION

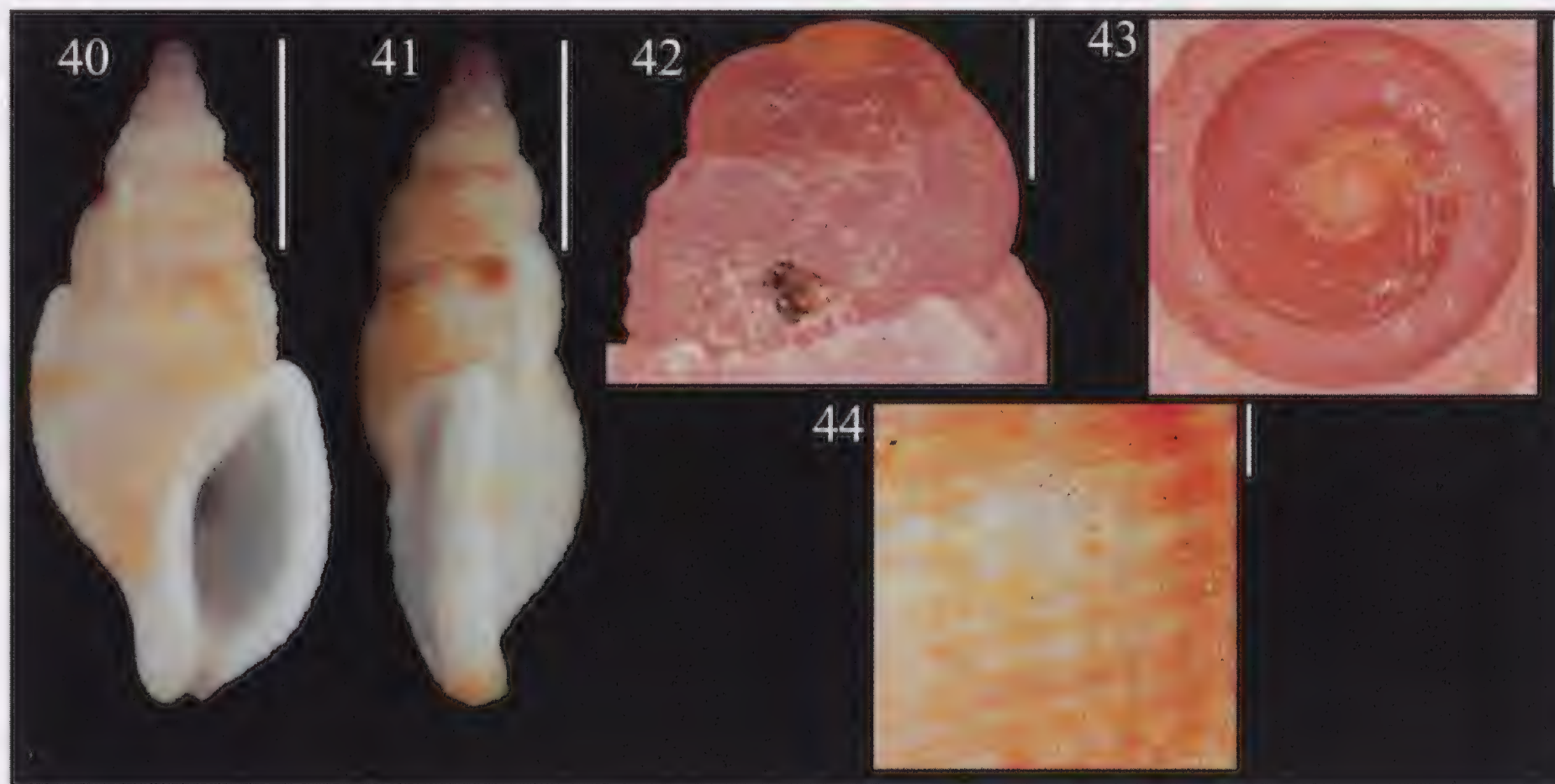
The present overview of *Tritonoharpa* from the western Atlantic demonstrates that there are doubts in the delimitation of most species and a more complete taxonomic revision is necessary. The newly described species, *T. curvapex*, is the most easily recognizable species presenting a distinctive protoconch shape (Figures 4, 9). The other species were rarely reported in the literature, except *T. lanceolata*, and were described based on a few or unique specimens. As commented by Verhecken (2011), who studied species of *Tritonoharpa* from the Philippines, the identification at species level in *Tritonoharpa* is rather complicated. Modica et al. (2011b: 692) also pointed about the difficulties in the taxonomy of *Tritonoharpa* species from shallow and deeper waters of the Pacific, Indian and Atlantic Oceans.

Although we recognized some diagnostic shell features of most of the *Tritonoharpa* from the western Atlantic, the scarcity of individuals hinders description of the variability of these features. *Tritonoharpa lanceolata* is supposedly the most common species, despite uncertainties about its taxonomy, and shows a variable teleoconch sculpture and color pattern (Beu and Maxwell, 1987). More recently, Lamy and Pointier (2017: 528, pl. 184, figs. 8–14) identified two nominal species (*T. bayeri* and *T. lanceolata*) and five morphotypes of *Tritonoharpa* sp. from Guadeloupe (Caribbean). These authors did not describe the diagnostic features of each morphotype, but based on the illustrations they possibly considered the different color patterns in the shells. At present, distinction of species by color pattern is a dubious approach.

Knowledge about the anatomy of *Tritonoharpa* is even more scarce, in the present study a few specimens of *T. leali* with soft parts were originally available for study. Unfortunately, part of these specimens was destroyed in the fire of “Museu Nacional” prior to anatomical studies. A *Tritonoharpa* species from the Philippines, erroneously cited as *T. antiquata* (Modica et al., 2009, 2011a, 2011b), is the only species of the genus of which the anatomy is known. More investigations on the anatomy of *Tritonoharpa* may help in the species delimitation.

Thus, based on the material examined here we can conclude that two species of *Tritonoharpa* certainly occur in Brazil: *T. curvapex* and *T. leali*. *Tritonoharpa leali* has a wider range of distribution in the Brazilian coast than previously reported in the literature, with occurrences in most of the Tropical Southwestern Atlantic province. However, it is possible that we were unable to recognize more than one species under the name *T. leali* in the present overview. The occurrence of *T. lanceolata* in Brazil needs clarifications.

The protoconch of all species of *Tritonoharpa* from the western Atlantic indicates a lecithotrophic development by



Figures 40–44. *Tritonoharpa janowski* Petuch and Sargent, 2011: holotype, USNM 1152535. **40.** Entire shell in frontal view. **41.** Entire shell in lateral view. **42, 43.** Detail of protoconch in lateral and apical views, respectively. **44.** Detail of teleoconch sculpture. Scale bars: **40, 41** = 5 mm; **42, 43** = 500 µm; **44** = 400 µm.

its diameter and number of whorls, which may explain the restricted geographic distribution of most species. *Tritonoharpa lanceolata* differs from the remaining species by its wider distribution, but as discussed above, this distribution is possibly over estimated based on the doubts about the identity of this species.

We hope that the illustrations of specimens, including type material whenever possible, and the gathering of data about western Atlantic *Tritonoharpa* will be useful for future studies about this genus, despite some of the tentative identifications in a confusing taxonomic scenario.

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Memorial to Warren O. Addicott—A remarkable student of Tertiary marine mollusks of the northeastern Pacific

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ABSTRACT

Warren Oliver Addicott (1930–2009) was a prolific molluscan paleontologist who produced in excess of one hundred publications, most of which deal with Tertiary fossil mollusks from western North America. In these publications he is credited with naming more than 80 new molluscan taxa, and recognizing and illustrating an additional 17 taxa that lacked sufficient material to be described as new. In addition, he is honored in having nine species named for him (eight mollusks and one arthropod).

"Warren Addicott was an exemplary paleontologist, far ahead of his peers, and willing to move into new areas and issues. He helped to supervise the Circum-Pacific Map Project, with many maps being put together and published under his tenure." (Ellen J. Moore, 2010, pers. comm., October 2010)

"...Warren Oliver Addicott (Ph.D. 1956), whose career with the Paleontology and Stratigraphy Branch of the U.S. Geological Survey in Menlo Park set new standards for monographic systematics, faunal and biostratigraphic documentation, and photographic illustration as well as initiating new insights and integration of molluscan research with active margin tectonics, refined climate curves, latitudinal distributions based on marine mollusks, increased radiometric age control on molluscan faunas, extension of molluscan paleontological interpretations into Alaska, and fostering exchange and collaboration with Japanese molluscan paleontologists." (Hickman, 2009.)

MEMORIAL

Warren Addicott was born in Fresno, California on February 17, 1930 to Irwin and Astrid Addicott. He was the eldest of two brothers, the younger being Alan Addicott. His formative years were spent in California where he attended Fresno High School in Fresno. At Fresno High School he played basketball making the local "Fresno Bee's [newspaper] All Yosemite League Basketball Team" (The Fresno Bee newspaper, February 27, 1946: 11; <https://www.newspapers.com/clip/>

8987288/the-fresno-bee-the-republican/). Afterward he attended Pomona College, where he was a student of the founding director of the geology department, Alfred O. Woodford. Warren graduated in 1951 with a BA in geology. A year later he received his M.A. from Stanford University's Hopkins Marine Station in Pacific Grove, California. Subsequently he attended the University of California at Berkeley where he received his Ph.D. from the Museum of Paleontology in 1956. While there, Warren completed his pioneering work on the Neogene Kern River deposits (1956) under J. Wyatt Durham, Charles W. Gilbert, and Ralph L. Langenheim.

In 1962, Warren joined the then-expanding Paleontology and Stratigraphy Branch of the U.S. Geological Survey (USGS) in Menlo Park, California. There he had a long and illustrious career focused on molluscan fossils of the eastern Pacific collaborating with colleagues in the Russian Far East, Japan, and later Spain. His first paper published by the USGS was with Jack G. Vedder, a renowned geologist in his own right, where they discussed the relationship between paleotemperature and Miocene mollusks in the Kern River area. Probably his most prominent publication is "Miocene Gastropods and Biostratigraphy of the Kern River Area, California" (Addicott, 1970d), which, 50 years later, remains a classic and an outstanding publication. In addition to his publications (listed below) Warren authored hundreds of Internal Reports on Referred Fossils (known as E&R's within the USGS) for other federal scientists and scholars around the world. John Barron (USGS) related a memory of Warren to us: when he first started his career at the USGS, he asked Warren for advice on how he should work. Warren suggested he divide his time into thirds, one third on service work (E&R's), one third on collaboration, and one third on his own research. This division of labor has similarly worked well for many USGS paleontologists over the years.

Warren was always willing to aid students and fellow scientists in their work. He sponsored the USGS postdoc of Judith Terry Smith (Smithsonian) for a year, although the two did not interact much. He helped Clifford M. Nelson with his dissertation on the gastropod genus



Figure 1. Warren O. Addicott. Photograph courtesy of Eric Addicott.

Neptunea. Nelson would later write a letter to Warren thanking him for his help; this letter is now preserved in the archives at the Museum of Paleontology, University of California, Berkeley. Richard G. Stanley (USGS) recalls

that when speaking with Warren in 1973 about his undergraduate thesis, he offered to loan him some fossils that Warren and Joe Clark (Indiana University of Pennsylvania) had collected from Richard's field site. Warren

was also interested in Richard's 1987 poster on right-lateral displacement of the San Andreas fault, which many other scientists disapproved of at the time. "I remember Warren as an exemplary and thoughtful scientist, and as a generous and kind human being," he related to us. Warren always answered letters that Lindsey Groves (Natural History Museum of Los Angeles County) sent him, as this latter worked on his masters thesis at California State University, Northridge. In addition, whenever possible he joined Robert J. McLaughlin and Dave Durham (both USGS) on field trips to Salinas Valley localities, and was always willing to look at "the most scruffy material." James C. Ingle, Jr. (Stanford University) tells of how he worked with Warren on several US-Japan projects dealing with Neogene paleontology around the Pacific Rim and that he later helped Jim obtain funding for field work on the Burica Formation in Panama. "He was a premier paleontologist, a wonderful colleague, and simply a great human being in every respect," he recalled.

In 1971, Warren became a consulting Associate Professor of Geology at Stanford University where he served as counsel for graduate students and supervised the University's Cenozoic and modern mollusk collections. Around 1980, Warren left the Branch for Paleontology and Stratigraphy, joining the Circum-Pacific Map Project (C-P M Project), because he was tired of having to ask for money from projects he helped. The goal of the C-P M Project was to gather together scientists from different parts of the world toward developing geologically significant maps throughout the Pacific region. Warren was appointed General Chairman of the C-P M Project in 1983, taking over from John A. Reinemund, who had been appointed Director in 1982. A few years later, in 1986, Warren retired from the USGS. That same year, he and his second wife Suzanne Aubin moved to Ashland, Oregon. After moving, Warren taught at the University of Southern Oregon from 1986 until his final retirement in 1990.

Throughout his career Warren was heavily involved in the broader scientific community. He became a fellow of the California Academy of Sciences, gave lectures and lead field trips for the American Association of Petroleum Geologists (AAPG) along with being editor of the Pacific Petroleum Geologists, a newsletter of the Pacific Section AAPG, and from 1971 to 1981 was a Trustee of Bulletins of American Paleontology (Paleontology Research Institute, Ithaca, New York). He was a founding member of the Western Society of Malacologists (1968) and is believed to have regularly attended meetings until at least 1975. In 1970, Warren was elected Secretary of the Paleontological Society, a position he held until 1976. Later, he was elected President of the Paleontological Society (1980). He also served on the editorial board for *The Veliger*, a quarterly published by the California Malacozoological Society, Inc.

When not working on research, Warren loved to garden. He was vice-president of the Peninsula Camelia Society in 1964 after moving to Menlo Park for his job at the USGS. In 1964 and again in 1968 he won several

camellia growing contests run by the local camellia society (Southern California Camellia Society, 1964: 22; 1968: 9–18), and wrote about the subject in the specialized literature (Addicott, 1967d: 27.)

He was also skilled at ceramics and a talented poet. Warren loved music, especially blues and jazz, and loved to compose his own music that he would play on the piano. He was married twice, first to Susanne Smith (1955–1972), and later to Suzanne Aubin (1976–2009). He left two children, Eric Addicott and Carol Kral, as well as two stepchildren, David LeDrew and Christine LeDrew-Johnson. Eric recounted to us: "Dad made it a priority to spend lots of time with my sister and me, and in many ways the divorce enhanced his relationship with us. He was always so loving and caring, and he always trusted my judgment and never really tried to guide or advise me too much. He introduced me to fishing, backpacking, cycling, and skiing, activities which I still do."

Warren was a world traveler and took an avid interest in other cultures. Not only did he travel for research-related reasons, but also for pleasure. He would even take time during overseas scientific conferences to visit scenic locations. For example during the 1971 Mediterranean Neogene Congress in Lyon, France, he visited the Rhone and Bordeaux basins in France.

After his retirement he moved to Ashland, where he continued to travel. In 1997, he wrote a letter to the Nu Alpha Phi fraternity at Pomona College (of which he was a member during his time there) noting that he and his second wife Suzanne had traveled to India in 1996 and stayed there for three months. He also worked as a realtor while in Ashland to keep busy.

Warren O. Addicott passed away July 11, 2009, with his wife Suzanne by his side, from complications of cancer. A hard worker and kind man, he named over 80 new molluscan taxa during his lifetime. His contributions to molluscan paleontology, and paleontology in general, solidified Warren Addicott's name as one of the great paleontologists of the late 20th Century.

NEW SPECIES NAMED IN HONOR OF WARREN

O. ADDICOTT

(names presented as in original combinations)

Mollusca

Bivalvia

Macoma addicotti Nikas (1977)

Mactromeris addicotti Kanno (1971)

Modiolus addicotti Moore (1984)

Mytilus (*Tumidimytilus*) *addicotti* Kafanov (1985) –

Holotype figured by Allison and Addicott (1976), pl. 3, fig. 9 [= *My. addicotti*]

Pitar addicotti Zinsmeister (1983)

Cephalopoda

Moroteuthis addicotti Clarke and Fitch (1979)

Gastropoda

Nassarius grammatus addicotti Adegoke (1969)

Scaphopoda

Cadulus (*Platyschides*?) *addicotti* Emerson (1957)

Arthropoda

Crustacea

Balanus addicotti Zullo (1979)

NEW MOLLUSCAN NAMES PROPOSED BY WARREN O. ADDICOTT

Bivalvia

Nucula salmonensis Addicott, 1966c

Platyodon colobus fowleri Addicott, 1966c

Propeamussium (*Propeamussium*) *leohertleini* Addicott, 1971a

Gastropoda

Acteon (*Rictaxis*) *weaveri* Addicott, 1970d

Aforia clallamensis tricarinata Addicott, 1966c

Antillophos woodringi Addicott, 1970d

Austrotrophon kernensis medialis (Addicott, 1970d)

Balcis lutzi Addicott, 1970d

Balcis petrolia Addicott, 1970d

Barkeria Addicott, 1970d – as a subgenus of *Cancellaria*

Calicantharus rancherianus Addicott, 1970d

Calicantharus woodfordi Addicott, 1970d

Calliostoma carsoni Addicott, 1970d

Calyptraea coreyi Addicott, 1970d

Cancellaria (*Crawfordina*) *kernensis* Addicott, 1970d

Cancellaria (*Euclia*) *circumspinoso* Addicott, 1970d

Cancellaria (*Euclia*) *ocoyana* Addicott, 1970d

Cancellaria (*Narona*) *birchi* Addicott, 1970d

Cancellaria galei Addicott, 1970d

Cancellaria keenae Addicott, 1970d

Catilon Addicott, 1965c – a subgenus of *Nassarius*

Crassispira olcesensis Addicott, 1970d

Crepidula bractea Addicott, 1970d

Crucibulum (*Dispotaea*) *papulum* Addicott, 1970d

Demonidia Addicott, 1965c – a subgenus of *Nassarius*

Epitonium (*Gyroscala*) *barkerianum* Addicott, 1970d

Epitonium (*Nitidscala*) *tedfordi* Addicott, 1970d

Forreria emersoni Addicott, 1970d

Gibbula (*Tumulus*?) *baileyi* Addicott, 1970d

Glyphostoma carinata Addicott, 1970d

Haminoea articensis Addicott, 1966c

Kelletia lorata Addicott, 1970d

Knefastia grarcesana Addicott, 1970d

Mangelia (*Notocytharella*?) *hartensis* Addicott, 1970d

Mitra (*Atrimitra*) *andersoni* Addicott, 1970d

Mitrella (*Columbellopsis*) *alta* Addicott, 1970d

Morula (*Morunella*) *granti* Addicott, 1970d

Nassarius (*Catilon*) *smooti* Addicott, 1965c

Nassarius hoquiamensis Addicott, 1966c

Nassarius (*Phrontis*) *harrellensis* Addicott, 1970d

Nassarius (*Phrontis*?) *posoensis* Addicott, 1970d

Nassarius (*Catilon*?) *salinasensis* Addicott, 1965c

Natica vokesi Addicott, 1966c

Nerita (*Theliostyla*?) *joaquinensis* Addicott, 1970d

Niso cottonwoodensis Addicott, 1970d

Ocenebrina clarki (Addicott, 1970d)

Odostomia (*Chrysallida*?) *sequoiana* Addicott, 1970d

Odontomia (*Menestho*) *repenningi* Addicott, 1970d

Polystira englishi Addicott, 1970d

Scaphander dollaris Addicott, 1966c

Sulcoretusa? *israeli* Addicott, 1970d

Tectionatica? *satsopensis* Addicott, 1966c

Tegula ellenae Addicott, 1966c

Tegula (*Omphalius*) *dalli arnoldi* Addicott, 1970d

Tegula (*Omphalius*) *laevis* Addicott, 1970d

Terebra (*Fusoterebra*?) *adelaidana* Addicott, 1970d

Terebra (*Strioterebrum*) *stirtoni* Addicott, 1970d

Trochotropis tricarinata Addicott, 1970d

Trochotropis (*Iphinoe*) *goweri* Addicott, 1966c

Turbonilla (*Chemnitzia*) *hannali* Addicott, 1970d

Turbonilla hormigacuesta Addicott, 1970d

Turbonilla (*Tragula*) *greenhomensis* Addicott, 1970d

Turbonilla (*Ptycheulimella*) *edisonensis* Addicott, 1970d

Turritella kernensis Addicott, 1970d

Turritella (*Idaella*) *vaquinana* Addicott, 1966c

Volvuella joaquinensis Addicott, 1970d

In addition to the species named by Warren (above) he recognized and illustrated a number of other potential new species. Unfortunately, these possible new species were not represented by sufficient material for him to name them and are listed in his publications simply as new species (n. sp.), or new species? (n. sp.?).

Bivalvia

Macoma n. sp. Addicott, 1969a [= *M. addicotti* Nikas, 1977]

Gastropoda

Astraea (*Pomaulax*) n. sp. Addicott (1970d)

Cancellaria n. sp. Addicott, 1969a [= *C. fergusonii* Carson, 1926]

Cancellaria n. sp.? aff. *C. alaskensis* Clark (1932), Addicott, 1980

Cancellaria (*Euclia*?) n. sp. Addicott, 1966c

Cymatium n. sp. Addicott, 1970d

Diodora (*Diodora*) n. sp. Addicott, 1970d

Diodora? n. sp. Addicott, 1970d

Neverita (*Glossaulax*) n. sp.? Addicott, 1970d

Odostomia (*Chrysallida*?) n. sp. Addicott, 1970d

Odostomia (*Evalea*?) n. sp. Addicott, 1970d

Oliva (*Oliva*) n. sp.? Addicott, 1970d

Terebra (*Strioterebrum*) n. sp.? Addicott, 1970d

Terebra (*Terebra*) n. sp. Addicott, 1970d

Triumphis? n. sp. Addicott, 1970d

Turbonilla (*Chemnitzia*) n. sp. Addicott, 1970d

Turbonilla (*Chemnitzia*?) n. sp. Addicott, 1970d

Turbonilla (*Pyrgiscus*) n. sp. Addicott, 1970d

PUBLICATIONS OF WARREN O. ADDICOTT

1953

Emerson, W.K., and W.O. Addicott. 1953. A Pleistocene invertebrate fauna from the southwest corner of San Diego County, California. San Diego Society of Natural History Transactions 11(17): 429–444.

1956

Addicott, W.O. 1956. Miocene stratigraphy northeast of Bakersfield, California. Berkeley. University of California, Ph.D. dissertation.

1958

Emerson, W.K., and W.O. Addicott. 1958. Pleistocene invertebrates from Punta Baja, Baja California, Mexico. *American Museum Novitates* 1909: 1–11.

1959

Addicott, W.O., and W.K. Emerson. 1959. Late Pleistocene invertebrates from Punta Cabras, Baja California, Mexico. *American Museum Novitates* 1925: 1–33.

1963

- a. Addicott, W.O. 1963. An unusual occurrence of *Tresus nuttallii* (Conrad, 1837) (Mollusca: Pelecypoda). *The Veliger* 5(4): 143–144.
- b. Addicott, W.O. 1963. Interpretation of the invertebrate fauna from the Upper Pleistocene Battery Formation near Crescent City, California. *Proceedings of the California Academy of Sciences, Fourth Series* 31(13): 341–347.
- c. Addicott, W.O., and J.G. Vedder. 1963. Paleotemperature inferences from late Miocene mollusks in the San Luis Obispo–Bakersfield area, California. *U.S. Geological Survey Professional Paper* 475C: C63–C68.

1964

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- b. Addicott, W.O. 1964. Pleistocene invertebrates from the Dune Terrace, western Santa Monica Mountains, California. *Bulletin of the Southern California Academy of Sciences* 63(3): 141–150.

1965

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- d. Addicott, W.O. 1965. Miocene macrofossils of the southeastern San Joaquin Valley, Calif. *U.S. Geological Survey Professional Paper* 525C: C101–C109.
- e. Durham, D.L., and W.O. Addicott. 1965. Pancho Rico Formation, Salinas Valley, California. *U.S. Geological Survey Professional Paper* 524A: A1–A22.
- f. Durham, D.L., and W.O. Addicott. 1965. Upper Miocene and Pliocene marine stratigraphy in southern Salinas Valley, California. *U.S. Geological Survey Bulletin* 1194: E1–E7.

1966

- a. Addicott, W.O. 1966. Late Pleistocene marine paleoecology and zoogeography in central California. *U.S. Geological Survey Professional Paper* 523C: C1–C21.
- b. Addicott, W.O. 1966. Miocene macrofossils of the southeastern San Joaquin Valley, California. *U.S. Geological Survey Professional Paper* 525C: C101–C109.
- c. Addicott, W.O. 1966. New Tertiary marine mollusks from Oregon and Washington. *Journal of Paleontology* 40(3): 635–646.
- d. Repenning, C.A., D.L. Jones, and W.O. Addicott. 1966. Geology of the Great Valley. *Mineral Information Service* 22(1): 3–6.

1967

- a. Addicott, W.O. 1967. Age of the Skooner Gulch Formation, Mendocino County, California. *U.S. Geological Survey Bulletin* 1254C: C1–C11.
- b. Addicott, W.O. 1967. Zoogeographic evidence for late Tertiary lateral slip on the San Andreas fault, California. *U.S. Geological Survey Professional Paper* 593D: D1–D12.
- c. Addicott, W.O. 1967. Paleontologic evidence for large post-early Miocene lateral slips on the San Andreas fault, California [abs.]. *Geological Society of America, Program, 63rd annual meeting, Santa Barbara, March 22–25, 1967*: 17.

1968

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1969

- a. Addicott, W.O. 1969. Late Pliocene mollusks from San Francisco Peninsula, California, and their paleogeographic significance. *Proceedings of the California Academy of Sciences, Fourth Series* 37(3): 57–93.
- b. Addicott, W.O. 1969. Late Pliocene marine mollusks from the northeastern Santa Cruz Mountains, California [abs.]. *Abstracts with Program for 1969 (Cordilleran Section)*, *Geological Society of America*, 3: 1.
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1970

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- e. Addicott, W.O. 1970. Tertiary climatic change in San Joaquin Basin, California – evidence from shallow-water mollusks [abs.]. *American Association of Petroleum Geologists Bulletin* 54(3): 561.
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1971

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Six new species of *Paciocinebrina* (Gastropoda: Muricidae: Ocenebrinae) from the northeast Pacific

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ABSTRACT

The western North American genus, *Paciocinebrina* Houart, Vermeij, and Wiedrick 2019, is both impressively speciose and phenotypically plastic, challenging the views of both lumpers and splitters. A recent study has revealed that the northeastern Pacific species of *Paciocinebrina* are distinct from the European type species, *Ocenebrina aciculata* (Lamarck, 1822) and other eastern Atlantic species, including *Ocenebra* Gray, 1847. Based on newly collected specimens and material already available, mostly from California, a spiral morphology comparison of six new species are herein described, including habitat and distribution records.

Additional Keywords: Gastropoda, Muricidae, Ocenebrinae, *Paciocinebrina*, new species, northeastern Pacific Ocean

INTRODUCTION

The predatory snail genus *Paciocinebrina* Houart, Vermeij, and Wiedrick, 2019 has long been a grouping of temperate snails chiefly restricted to the northeast Pacific and similar in appearance to northeastern Atlantic and Mediterranean species of *Ocenebrina* Jousseaume, 1880. Molecular studies (Barco et al., 2017) support these genera as distinct lineages, both having radiations of diversity. Houart et al. (2019) used morphological and biogeographic comparisons to provide a faunal list and to describe several new species from the southern range of *Paciocinebrina*. *Paciocinebrina* is one of about 33 recognized genera within the muricid subfamily Ocenebrinae Cossmann, 1903 (Molluscabase eds., 2020). Voucher material examined range from intertidal to subtidal (to 686 m) habitats, and were reported from as far north as the Kenai Peninsula, Kenai-Cook County, Alaska (59° N) and as far south as Bahía Magdalena, Baja California Sur,

Mexico (24° N). Assuming that the LACM collections examined accurately reflect distributional patterns, these snails are much more abundant in the northern portion of the range but are still present at moderate densities south of San Luis Obispo County, California.

The diversity of this group has long been debated, highlighted by the conflicted views of Radwin and D'Attilio (1976) and Fair (1976). Shell and radular morphology have been the basis of *Paciocinebrina* descriptions (Radwin and D'Attilio, 1971; 1976), with morphological characters having a historical perspective, embraced by malacologists in the diagnosis of molluscan species and higher taxa in systematic studies (Ponder and Lindberg, 1997).

The reproductive life histories of this group are poorly understood and known from very few studies (Merle et al., 2011: 23). Paleobiologists (Jablonski and Lutz, 1983) have found that morphological features in the protoconch sculpture of marine benthic gastropods are a result of their mode of development (Bouchet and Strong, 2010: 65; Merle et al., 2011: 23). The use of this feature to determine species delineation, biodiversity, and life history patterns has been broadly used for neogastropods (Shuto, 1974; Bouchet, 1990), including studies on muricids (Radwin and D'Attilio, 1976; D'Attilio, 1980; 1981; Myers and D'Attilio, 1986; Merle et al., 2011: 17, 23) and conoideans (Powell, 1966: 6; Bouchet, 1990). The uniform possession of paucispiral protoconchs in eastern Pacific *Paciocinebrina* species was noted by McLean (1996: 80) and indicates that the mode of reproduction across the taxon is by intracapsular development. Hansen (1980), Jablonski and Lutz (1983), and Jablonski (1986) found higher speciation and extinction rates in this mode of development, which seems to parallel the radiation and fossil record of this group (Marshall et al., 2012; Nützel, 2014). Fluctuating sea level and temperature changes likely contributed to higher periods of diversification, whether in warm periods (Mayhew et al., 2012) or cold periods (Davis et al., 2016), as reflected in the Neogene

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and Quaternary fossil record of California. Modes of larval dispersal may have been under selection by the strong currents seen in the eastern Pacific, a model discussed by Brown (2014).

Several contributing factors are likely the cause of species within this genus to inhabit rocky substrate, whether intertidal or subtidal. Ecological and physiological factors such as reproduction, feeding, and ecological niches are likely influenced by habitat selection by these gastropods. Abbott (1968: 126) illustrated western Atlantic muricid egg capsules, which appear to be similar in appearance to northeastern Pacific *Paciocinebrina* species. Laboratory studies by Spight et al. (1974: 234) detailed egg capsule laying on rocks by *Paciocinebrina interfossa* (Carpenter, 1864), with Griffith (1967: 69) noting some eastern Pacific muricids known to guard eggs during incubation. This reproductive process appears to limit connectivity between populations, as long spanning, intertidal and subtidal sandy shorelines tend to isolate rocky reefs in the eastern Pacific, which could restrict migration between these populations, isolating them to rocky habitats. Diet, feeding preference, and food abundance likely play a role in habitat selection. Species within this group are carnivorous and feed by means of radula and an accessory boring organ, which in combination, are capable of drilling through a prey's hard flesh or exoskeleton (Vermeij, 1993: 105, 108; McLean, 2007: 740; Bertsch and Rosas, 2016: 216–217). The preferred diet of *Paciocinebrina* species is primarily comprised of sessile barnacles, mollusks, and other invertebrates restricted to rocky habitats.

Paciocinebrina species have been reported as feeding or associated with the mantle of the gumboot chiton, *Cryptochiton stelleri* (Middendorff, 1846) (Talmadge, 1975; Abbott and Haderlie in Morris et al., 1980: 277), barnacles (Rice, 1971: 48; Abbott and Haderlie, 1980: 277; Palmer, 1988; McLean, 2007: 740; McLean, 1996: 78; Bertsch and Rosas, 2016: 216; Merle et al., 2011: 24), limpets (Palmer, 1988; Bertsch and Rosas, 2016: 216), bivalves (Palmer, 1988; McLean, 2007: 740; McLean, 1996: 78; Merle et al., 2011: 24), other mollusks (Palmer, 1988; Abbott and Haderlie, 1980: 277; Merle et al., 2011: 24) and the shelled polychaete worm, *Spirorbis* (Palmer, 1988: 192).

New species descriptions are based on the analysis of type material from the California Academy of Sciences (CASIZ), Natural History Museum of Los Angeles County (LACM), San Diego Natural History Museum (SDNHM), National Museum of Natural History, Smithsonian Institution (USNM), University of California, Museum of Paleontology (UCMP), several private collections, and the collection of subtidal and intertidal specimens ranging from Devil's Gate, Humboldt Co. (40°N) to Laguna Beach, Orange Co., California (33°N). A revision of *Paciocinebrina* is presented in Wiedrick (thesis) including the chresonymy, synonymy, biodiversity, biogeography, and ecology of known nominal taxa based on existing literature, the aforementioned specimens, and molecular data.

MATERIALS AND METHODS

INSTITUTIONAL ABBREVIATIONS

CASIZ: California Academy of Sciences, Invertebrate Zoology, San Francisco, California, U.S.A.
LACM: Natural History Museum of Los Angeles County, Malacology Department, California, U.S.A.
NHMUK: Natural History Museum of the United Kingdom, London, England, U.K.
SDNHM: San Diego Natural History Museum, San Diego, California, U.S.A.
SGW: collection of Shawn G. Wiedrick
UCMP: University of California, Museum of Paleontology, Berkeley, California, U.S.A.
USNM: National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A.
ZIN: Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia

SPIRAL MORPHOLOGY ABBREVIATIONS

Terminology used to describe the spiral cords and the internal denticles of the outer lip (based on Merle, 1999; 2001; 2005; Merle and Houart, 2003):

ab: abapical (or abapertural); **abis:** abapical infrasutural secondary cord (on subsutural ramp); **ABP:** abapertural primary cord on the siphonal canal; **abs:** abapertural secondary cord on the siphonal canal; **ad:** adapical (or adapertural); **adis:** adapical infrasutural secondary cord (on subsutural ramp); **ADP:** adapertural primary cord on the siphonal canal; **ads:** adapertural secondary cord on the siphonal canal; **IP:** infrasutural primary cord (primary cord on subsutural ramp); **MP:** median primary cord on the siphonal canal; **ms:** median secondary cord on the siphonal canal; **P:** primary cord; **P1:** shoulder cord; **P2–P6:** primary cords of the convex part of the teleoconch whorl; **s:** secondary cord; **s1–s6:** secondary cords of the convex part of the teleoconch whorl; **SP:** subsutural cord; **t:** tertiary cords; **D1–D6:** abapical denticles; **ID:** infrasutural denticle.

RESULTS

SYSTEMATICS

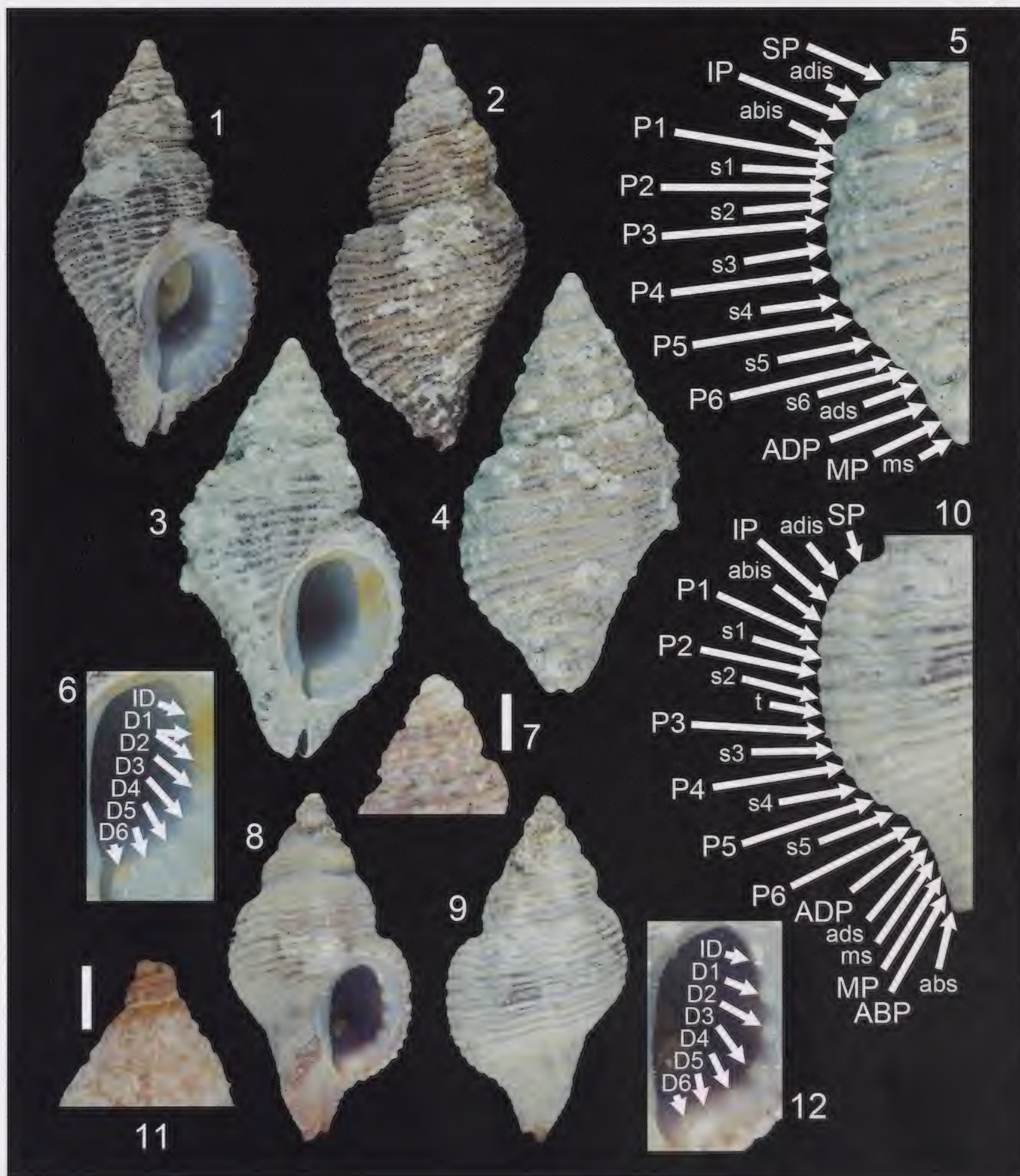
Muricidae Rafinesque, 1815
Ocenebrinae Cossmann, 1903

Genus *Paciocinebrina* Houart, Vermeij and Wiedrick, 2019

Type Species: *Tritonium (Fusus) luridum* Middendorff, 1848: 244, by original designation, Recent, Sitka, Alaska (Syntype, ZISP 62131).

Remarks: The complete faunal list and description was provided by Houart et al. (2019: 209–210). Additional new species are proposed below.

Paciocinebrina bormannae new species (Figures 8–12)



Figures 1–12. *Paciocinebrina* species. **1–7.** *Paciocinebrina grandilurida* new species. **1–2.** Shelter Cove, California, intertidal on rock, length 26.2 mm, width 13.5 mm (SGW 115). **3–4.** Holotype, Shelter Cove, California, intertidal, length 27.0 mm, width 15.0 mm (LACM 3761). **5.** Spiral cords morphology. **6.** Apertural denticles morphology. **7.** Protoconch, scale bar: 1.0 mm (SGW 116). **8–12.** *Paciocinebrina bormannae* new species. **8–9.** Holotype, Cayucos, California, on rocks at low tide, length 22.4 mm, width 12.3 mm, (LACM 3760). **10.** Spiral cords morphology. **11.** Protoconch, scale bar: 1.0 mm (SGW 117). **12.** Apertural denticles morphology.

CHRESOONYMY

Ocenebra lurida aspera.—Smith and Gordon, 1948: 189.
Ocenebra lurida.—Abbott and Haderlie, 1980: 277–278,
 fig. 13.76.

Ocenebrina foveolata.—Liff-Grieff, 2006: 4, lower right
 figures.

Description: Large for genus, holotype 22.4 mm in length, width 12.3 mm. Shell robust, thick, shape broad, elongate-ovate, spire angle variable, siphonal canal narrow, short, acutely tapered, color rustic brown, with dark brown incised lines between cords, aperture white, blue overtones, siphonal canal creamy tan. Protoconch bulbous with subtle carination, shoulder and median cord abruptly formed, converged by vertical ribs of first teleoconch whorl, clathrate in appearance, later cords strong, overriding ribs, fimbriations vaulted, close set, extremely fine and low profile in interspaces. First teleoconch whorl with P1, P2 spiral cords, second with P1 and P2 cords, starting IP and s1 cords, third whorl with IP, P1, s1, P2 cords, starting adis and s2 cords, fourth with adis, IP, P1, s1, P2, s2 cords, starting P3 cord, final whorl with SP, adis, IP, abis, P1, s1, P2, s2, t, P3, s3, P4, s4, P5, s5, P6, ADP, ads, ms, MP, ABP and abs spiral cords, nine faint axial ribs on final whorl. Apertural denticles morphology with ID and six primary denticles, ID denticle extremely indistinct, D1 denticle weak, D2–D4 denticles stronger, final denticles slightly weaker. Aperture elongate ovate, moderate in size, lip of aperture thick, edge sharp, strongly projecting, parietal wall weak posteriorly, thicker anteriorly of columellar wall, siphonal canal comparatively thin, tapered towards anterior end.

Type Material: Holotype LACM 3760, length 22.4 mm, width 12.3 mm.

Type Locality: Cayucos, San Luis Obispo County, California, (35°26'40" N, 120°56'42" W), on rocks at low tide.

Other Material Examined: Two specimens, 12.1–38.1 m, Carmel Submarine Canyon, north end San Jose Creek Beach, Monterey County, California (36°31'59" N, 121°55'59" W), collected by J.H. McLean, 1960–1964 [LACM 1960–24.105]; two specimens, Monterey, Monterey County, California [LACM 151093]; four specimens, intertidal on shale ledges, west of Cayucos Creek, San Luis Obispo County, California (35°26'48" N, 120°54'29" W), collected by P.I. LaFollette, 11 December 1977 [LACM 1977–112.48]; four specimens, Cayucos, San Luis Obispo County, California, collected by Bormann [LACM 72468]; one specimen, intertidal, Dinosaur Cave, Shell Beach, San Luis Obispo County, California (35°9'11" N, 120°40'36" W), collected by P.M. Oringer, 19 December 1968 [LACM 1968–48.23]; six specimens from Shell Beach, San Luis Obispo County, California (35°9'24" N, 120°40'36" W), intertidal on shale ledges, collected by J.H. McLean, 1961–1963 [LACM 1961–11.50]; six specimens, near Arroyo Grande, San Luis Obispo County, California [LACM 59600]; three specimens, San Luis Obispo County, California [LACM 59620]; one specimen, 3.2 km north of

Avalon, Santa Catalina Island, California Channel Ids., California (33°23'59" N, 118°22'0" W), collected by J.H. McLean, 29 April 1962 [LACM 1962–5.31].

Distribution: Carmel Submarine Canyon, Monterey Co., California (36°) to Avalon, Santa Catalina Island, California Channel Ids., California (33°N); primarily on low intertidal rocks, large rock overhangs and undersides of giant boulders, to 38.1 m.

Remarks: The spiral morphology of the initial whorl are identical (P1 and P2) to various other *Paciocinebrina* species, with distinct s2 cord in the second whorl of *P. bormannae*, third whorl with adis cord, a feature not seen in comparable species, fourth whorl similar to *Paciocinebrina munda* (Carpenter, 1864), with P3 cord absent in that species, final whorl of *P. bormannae* with SP, abis, s4, ads, ms, abs cords and s6 cord absent, all characters not seen in *P. munda* (Figures 56–59). Superficially similar to the more northern species, *P. grandilurida* new species, but is lighter in coloration, has a less acute spire, one additional axial rib on final whorl and a different spiral cord morphology with *P. bormannae* having an additional t cord after s2 and ABP, abs cords on final whorl (Figures 5, 10).

Etymology: Named in honor of the late Mary Bormann, a collector of various *Paciocinebrina* species, who also had a particular passion for this group of west coast muricids.

***Paciocinebrina grandilurida* new species**
 (Figures 1–7)

Description: Shell large for genus, holotype length 27.0 mm, width 15.0 mm. Shape acute rhomboid, outer lip projecting, thick, spire acute, siphonal canal moderately long, color dark brown to black, interspaces lighter in appearance, canal face white, aperture interior often with blue overtone. Initial protoconch whorl low laying, bulbous, tabulation faint, shoulder and median cords well established, ribs becoming well developed, first teleoconch whorl with overriding spiral cords, further whorls forming large, thick, tightly set cords, final whorl surface heavily scabrous, especially between cords, obscurely clathrate. First teleoconch whorl with P1, P2 spiral cords, second with P1, P2 cords, starting IP cord, third whorl with IP, P1, P2 cords, starting s1, s2 cords, fourth with IP, P1, s1, P2, s2 cords, starting adis, abis cords, final whorl with SP, adis, IP, abis, P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, s6, ads, ADP, MP, ms spiral cords, eight very faint, broadly spaced axial ribs on final whorl. Aperture elongate ovate, with ID, D1 split and five additional denticles, columellar lip wide, recessed into previous whorl, siphonal canal rather short, pseudumbilicus faint.

Type Material: Holotype LACM 3761, length 27.0 mm, width 15.0 mm.

Type Locality: Shelter Cove, Humboldt County, California, (40°1'24" N, 124°4'24" W) on rocks at low tide.

Other Material Examined: 12 specimens, intertidal, near Machi Brothers Resort, Shelter Cove, Humboldt

County, California (40°01'29" N, 124°04'00" W), collected by P. I. LaFollette, 19–20 July 1970 [LACM 70–70.40]; four specimens, intertidal on rocks, Van Damme State Park, Little River, Mendocino County, California (39°17'42" N, 123°47'48" W), collected by J.H. McLean, 22 February 1964 [LACM 64–8.34]; two specimens, intertidal, Albion, Mendocino County, California (39°14'30" N, 123°46'30" W), collected by J.H. McLean, 11 November 1962 [LACM 62–15.30]; two specimens, intertidal, 0.8 km south of Fort Ross, Sonoma County, California (38°30'42" N, 123°13'59" W), collected by J.H. McLean, 28 December 1963 [LACM 63–57.23].

Distribution: Shelter Cove, Humboldt Co., California (40°N) to Fort Ross, Sonoma Co., California (38°N); low to mid intertidal zone, on rock reefs, undersurfaces of large boulders and on the girdle of the gumboot chiton, *Cryptochiton stelleri* (Middendorff, 1846).

Remarks: The first three whorls are identical to *Paciocinebrina munda* (P1, P2; IP, P1, P2; IP, P1, s1, P2, s2), with abis cord of fourth whorl absent in *P. munda*. See *P. bormannae* section for comparisons to this species. Talmadge (1975: 414), Abbott and Haderlie (1980) and McConnaughey and McConnaughey (1985: 358) reported the feeding of *Paciocinebrina lurida* (Figures 60–63) on the gumboot chiton, *Cryptochiton stelleri* (Middendorff, 1846), although field observations from Shelter Cove have exclusively been by the larger *P. grandilurida*, despite the mass presence of *P. lurida* at that locality.

Etymology: In reference to the large size and similarities to the smaller *Paciocinebrina lurida* (Middendorff, 1848), *grandi-* meaning grandiose, *lurida* in reference to that other species, gender feminine.

***Paciocinebrina mininterfossa* new species**
(Figures 13–18)

CHRESONYMY

Ocenebra interfossa.—Rice, 1971: pl. 17, fig. 98.

Type Material: Holotype LACM 3762, length 13.1 mm, width 6.1 mm (*ex* SGW 114).

Type Locality: China Rock, Seventeen Mile Drive, Monterey County, California, (36°36'10" N, 121°57'42" W), on rocks at low tide.

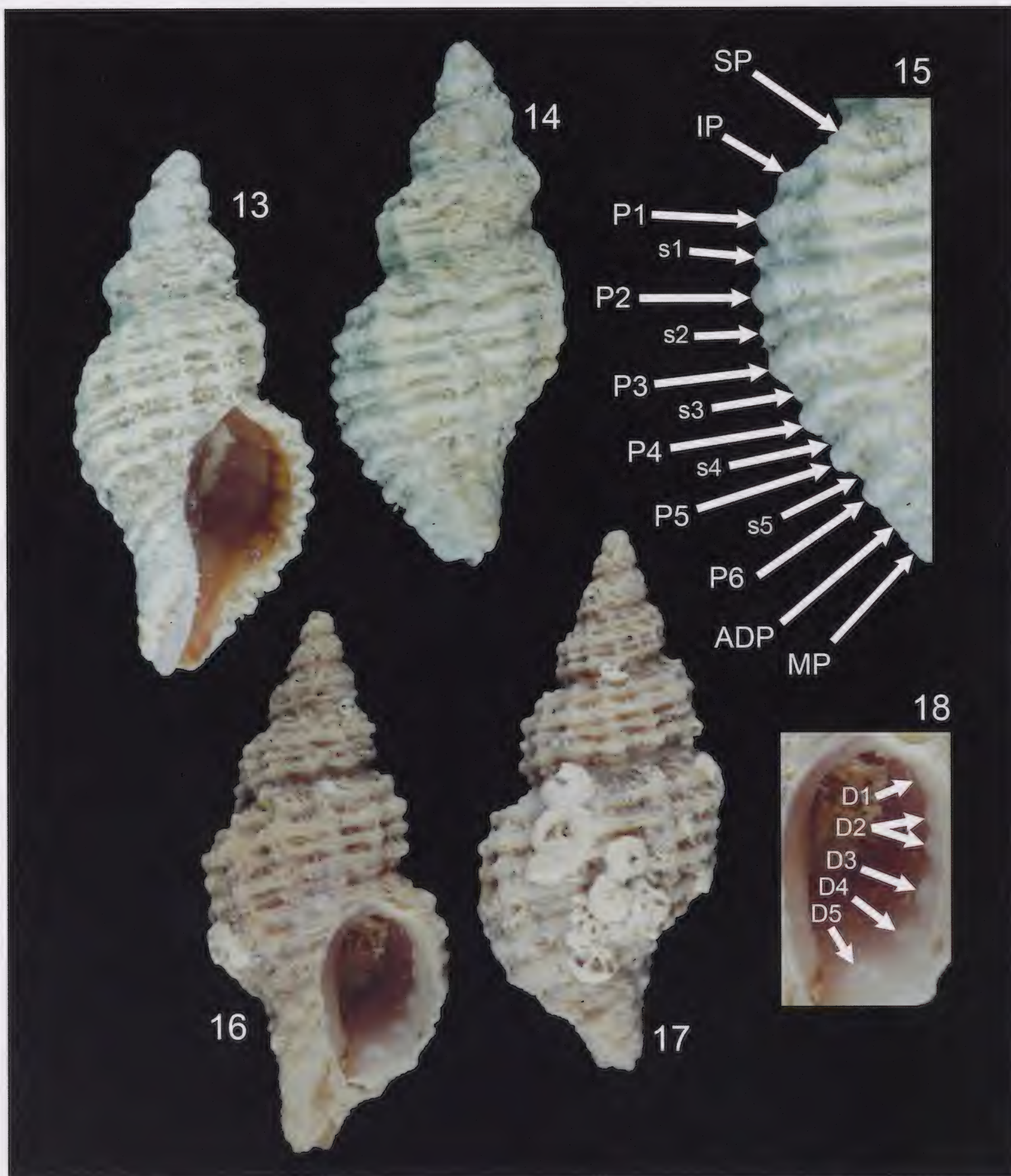
Other Material Examined: Five specimens, Crescent City, Del Norte County, California, collected by E. P. Chace [LACM 72475]; two specimens, 18 m, Isle of St. James, North Farallon Islands, California (37°45'40" N, 123°5'57" W), collected by R.W. Schmieder, R/V CORDELL EXPLORER, 14 September 1991 [LACM 1991–177.19]; two specimens, intertidal on rocks, south side of Point Joe, Seventeen Mile Drive, Monterey County, California (36°36'29" N, 121°57'29" W), collected by P.I. LaFollette, June 1962 [LACM 1962–43.4]; 10 specimens, intertidal, Pacific Grove, Monterey County, California (36°37'22" N, 121°54'34" W), collected by J.H. McLean, 1959–1964

[LACM 1959–12.63]; one specimen, intertidal on *Phyllospadix* roots, Hopkins Marine Station, Pacific Grove, Monterey County, California (36°37'30" N, 121°54'00" W), collected by J.H. McLean, 1 December 1962 [LACM 1962–16.17]; three specimens, Pacific Grove, Monterey County, California [LACM 151066].

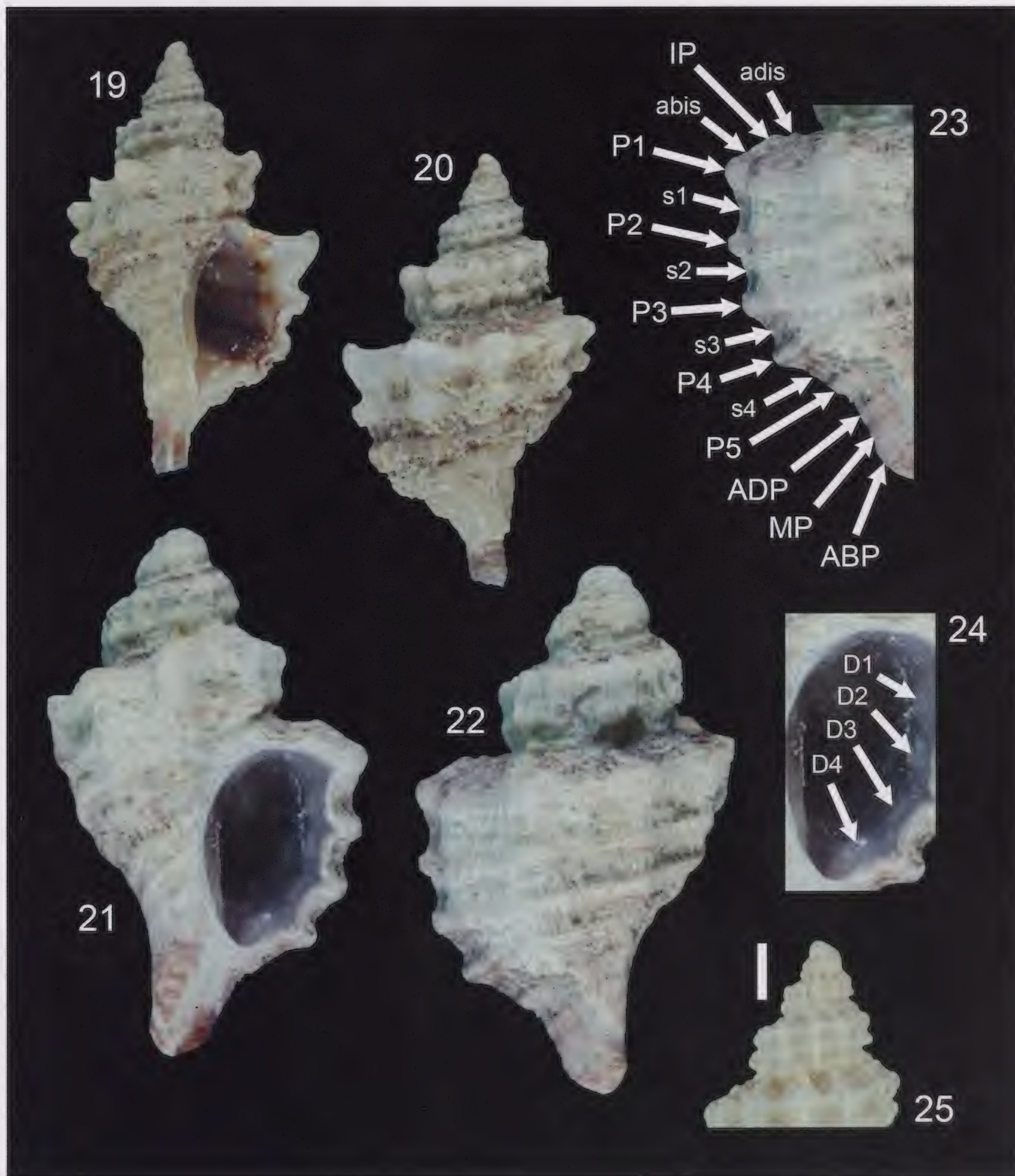
Distribution: Crescent City, Del Norte Co., California (41° N) to China Rock, Seventeen Mile Drive, Monterey, Monterey Co., California (36°N); primarily at low to mid-intertidal zones on rocks, near dense mats of purple algae, as noted on one LACM record from near the surfgrass, *Phyllospadix*, 1 subtidal lot at 18 m.

Description: Shell small for the genus, holotype length 13.1 mm, width 6.1 mm. Shell elongate, profile narrow, slenderly rhomboid, whorls ovate, tall, sutural indentations weak, size small, but robust, ribs subtle, scabrous sculpture of even width throughout entire length of shell, color dingy white, occasionally with light brown band on P2 cord below shoulder, outer lip of aperture dull white, columellar and parietal walls and interior flushed with purplish brown. Spire acute, protoconch bulbous, worn in nearly all specimens examined. Initial whorl somewhat flattened, wide spanning, half set into proceeding whorl, rotund, becoming shouldered by cord further into whorl than most other *Paciocinebrina* species. Median cord strong, slightly more projecting initially, becoming of equal strength and pseudo-clathrate, spiral cords becoming projected nodes at intersection of axial ribs. Shape of siphonal canal moderately small, tapering. First teleoconch whorl in holotype with P1, P2 cords, second with P1, P2 cords, starting IP cord, third with P1, P2 cords, starting, s1 cord, fourth whorl with IP, P1, s1, P2 cords, starting s2 cord, final whorl with SP, IP, P1, s1, P2, s2, P3, s3, P4, s4, P5, s5, P6, ADP, MP spiral cords and eleven narrow, but widely spaced axial ribs. Aperture consistently with weak D1, D2 (split), D3, D4, D5 denticles, strongest centrally, split D2 denticles weak in small sized specimens. Aperture moderately sized, ovate, posterior end squarer in shape, lip heavily developed and thick at subsutural ramp on final varices, slightly slimmer at shoulder, thinning towards anterior end, parietal wall extremely thin at top, wider anteriorly, slightly thicker at columellar wall, terminated by a twist near anterior end.

Remarks: The initial three teleoconch whorls are identical to *Paciocinebrina minor* (Dall, 1919) (Figures 44–47), with *P. mininterfossa* having adis, abis, s1, s2, s3, s4, s5 and P6 cords on the fourth whorl, characters absent in *P. minor*. This species is very small compared to the similar appearing species, *P. interfossa* (Figures 64–67), of which many specimens have been haphazardly mixed into LACM lots labelled as such, a likely assumption is that workers simply presumed a juvenile state in this smaller species. Additionally, this taxon is a dingy white, not brown, has thicker and much looser sutural scabrosity and a different spiral morphology. A specimen figured by Rice (1971), and identified as *P. interfossa*, seems to match the holotype of this species and



Figures 13–18. *Paciocinebrina mininterfossa* new species. **13–14.** China Rock, California, on intertidal rock, length 12.7 mm, width 6.3 mm, (SGW 118). **15.** Spiral cords morphology. **16–17.** Holotype, China Rock, California, on intertidal rock, length 13.1 mm, width 6.1 mm, (LACM 3762). **18.** Apertural denticles morphology.



Figures 19–25. *Paciocinebrina murphyorum* new species. **19–20.** Shell Beach, California, length 9.6 mm, width 5.6 mm (SGW 119). **21–22.** Holotype, Jade Cove, California, on rock at 14.6 m, length 11.7 mm, width 7.2 mm, (LACM 3763). **23.** Spiral cords morphology. **24.** Apertural denticles morphology. **25.** Protoconch, scale bar: 1.0 mm (SGW 120).

is here included, despite Rice (1971) neglecting to provide a specific locality of the figured specimen. This species has been observed in the field as feeding on *Barleeia* species.

Etymology: Gender feminine in the nominative case, *mini-* meaning a miniature version of *P. interfossa*, meaning having ditches among itself, in reference to the sculpture of that species.

***Paciocinebrina murphyorum* new species**
(Figures 19–25)

CHRESONYMY

Ocenebra interfossa clathrata.—Bormann, 1946: 39, pl. 4, fig. 1, 3.

Description: Shell small for genus, holotype length 11.7 mm, width 7.2 mm. Shape rhomboid, severely indented at whorl base, siphonal canal moderately long, narrow, whorls tabulate, sculpture clathrate, of thick intersecting cords and ribs, color chalky white with dark brown bands at suture to mid-subsutural ramp, and posteriorly before cords P3 through P4, aperture interior usually brown or brownish purple, parietal wall lighter in coloration, somewhat thin, twisted anteriorly. Initial protoconch whorl upward projecting, rapidly downward angled in shoulder cord, anteriorly tabulate, cords equal in strength, rectangularly clathrate at rib intersections, deep squarish pits on final whorl, early whorl growth lines faint, crispate scales tightly spaced on final whorl, less evident in pits. First two teleoconch whorls with P1, P2 cords, third with P1, P2 cords, starting P3 cord, fourth whorl with adis, IP, abis, P1, s1, P2, s2, P3, s3, P4, s4, P5, ADP, MP, ABP spiral cords, nine strong, widely spaced axial ribs, projecting at shoulder on final whorl. Aperture somewhat small, ovate with D1–D4 denticles, outer lip projecting, lip thickened, parietal wall closely attached, narrow, siphonal canal long, spindle-like from basal indentation.

Type Material: Holotype LACM 3763, length 11.7 mm, width 7.2 mm.

Type Locality: Jade Cove, Big Sur, Monterey County, California, (35°54'46" N, 121°28'29" W), on rock at 14.6 m.

Other Material Examined: Two specimens, Roller Bay, intertidal rocks, Hope Island, Vancouver Island, Rupert District, British Columbia, Canada (50°55'36" N, 127°57'5" W), collected by J.H. McLean, 22 May 1963 [LACM 1963–31.22]; four specimens at 9–15 m, 100 m inshore of buoy at Point Delgado, Humboldt County, California (40°0'29" N, 124°04'00" W), collected by C.C. Swift, R/V SEARCHER, 29 July 1971 [LACM 1971–107.12]; one specimen at 0.3 m on rocks, northwest of Pico Creek, San Simeon Village, San Luis Obispo County, California (35°36'55" N, 121°9'4" W), collected by P.I. LaFollette, 8 August 2006 [LACM 2006–28.1]; three specimens, Cayucos, San Luis Obispo County, California, collected by R. and M. Bormann [LACM 72480]; six specimens, intertidal on shale ledges, Shell Beach, San Luis Obispo

County, California (35°9'24" N, 120°40'36" W), collected by J.H. McLean, 1961–1963 [LACM 1961–11.48]; 12 specimens, intertidal on shale ledges and boulder reef, 0.4 km northwest of South Point, Shell Beach, San Luis Obispo County, California (35°9'18" N, 120°40'29" W), collected by P.I. LaFollette, 10 December 1977 [LACM 77–111.44]; one specimen, intertidal, Avila Beach, San Luis Obispo County, California (35°10'59" N, 120°43'59" W), collected by P.M. Oringer, 28 July 1968 [LACM 1968–37.36]; two specimens, San Nicolas Island, California Channel Ids., California, MacGinitie collection, 17–19 July 1962 [LACM 59601].

Distribution: Hope Island, Vancouver Island, British Columbia (50° N) to San Nicolas Island, California Channel Ids., California (33° N); on and under intertidal rocks, in gravel, rarely at shallow subtidal depths to 14.6 m.

Remarks: The initial three whorls are identical to *Paciocinebrina minor*, with *P. murphyorum* having adis, abis, s1, s2, s3 and s4 spiral cords on fourth whorl, characters absent in *P. minor*. This species superficially resembles *P. atropurpurea* (Carpenter, 1865) but has a different morphology (Figures 52–55) than *P. murphyorum* (Figures 23–24). Bormann (1946: pl. 4, fig. 1, 3) figured a specimen of this species under the name *clathrata*, now known as a synonym of *P. atropurpurea* (Houart et al., 2019: 209).

Etymology: Named in the genitive case for the surname Murphy, a name representing Brendan and William Murphy, two individuals completely unknowingly of one another, but coincidentally with same last name. Brendan, a dear friend and high school colleague of the senior author, facilitated the first visit to the type locality of this species, a site where several specimens had subsequently been collected and examined for this description. William Murphy, a dear friend of the senior author's father, was gracious enough, along with wife Donna, to host Mr. Wiedrick at their residence in Humboldt County, an opportunity that afforded Mr. Wiedrick to conduct research in northern California field sites. Specimens sampled and identified as *P. grandilurida* from Shelter Cove, the city in which Mr. and Mrs. William Murphy resides, is also the type locality of that new species, the only location where this species was acquired and analyzed for spiral morphology.

***Paciocinebrina pseudopusilla* new species**
(Figures 26–36)

CHRESONYMY

Ocenebra interfossa.—Radwin and D'Attilio, 1976: pl. 20, fig. 11.

Description: Shell very small for genus, holotype worn, length 7.5 mm, width 5.8 mm, paratype juvenile, length 5.4 mm, width 3.0 mm. Shell ovate rhomboid, siphonal canal short, sculpture clathrate, axial ribs somewhat narrow, cord thickness moderate, interspaces squarish, large, color white to tan, pits slightly browner, occasionally

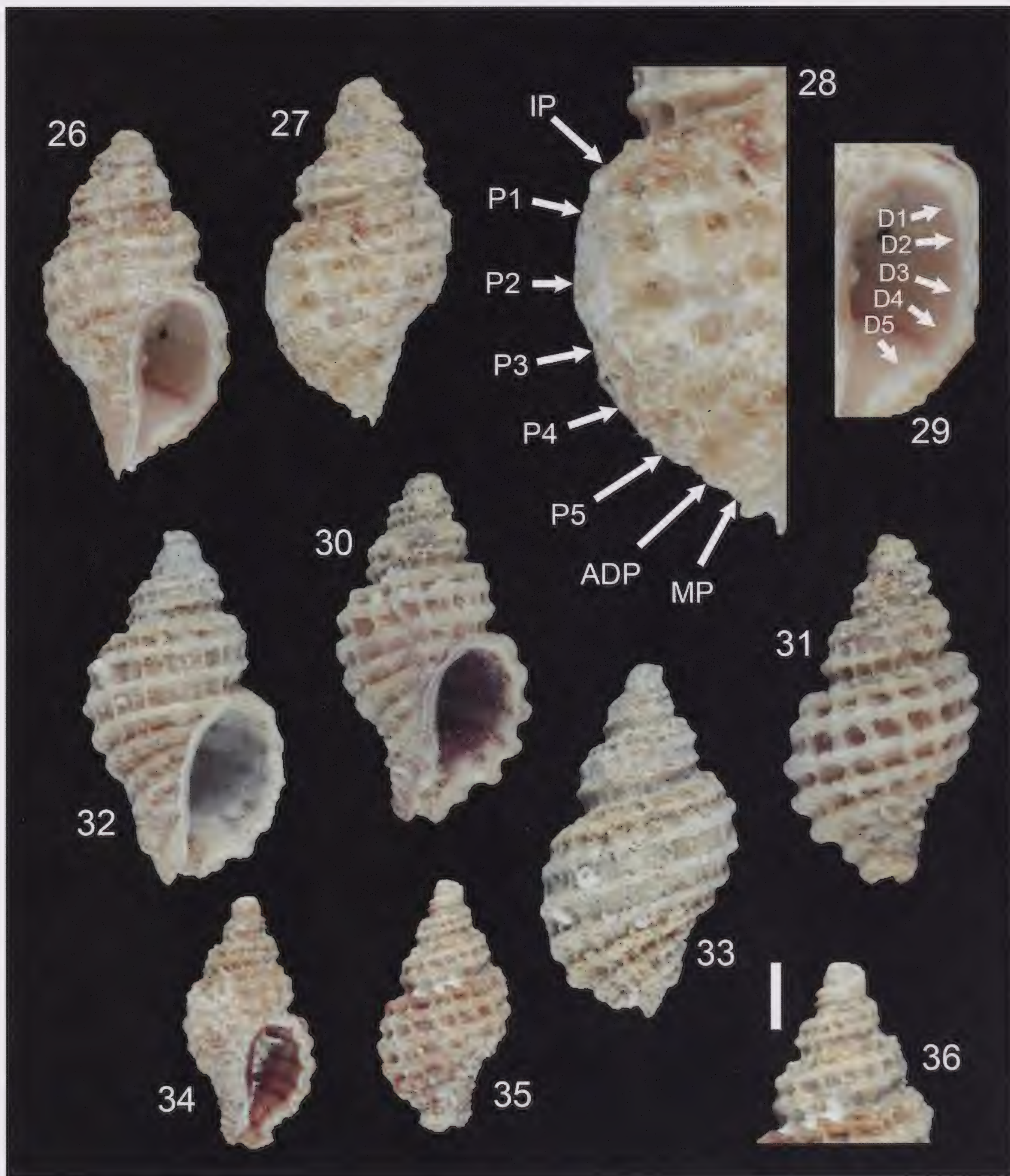


Figure 26–36. *Paciocinebrina pseudopusilla* new species. **26–27.** Holotype, China Rock, California, length 7.5 mm, width 5.8 mm (LACM 3764). **28.** Spiral cords morphology. **29.** Apertural denticles morphology. **30–31.** *P. pseudopusilla*, Neah Bay, Washington, length 7.5 mm, width 4.3 mm (SGW 121). **32–33.** Punta Popotla, Baja California, Mexico, length 7.6 mm, width 4.3 mm (SGW 122). **34–35.** Paratype, Jade Cove, California, on rock at 14.6 m, length 5.4 mm, width 3.0 mm, (LACM 3766). **36.** Protoconch, scale bar: 1.0 mm.

with sienna brown blotches on IP cord and/or P1 cord white, rarely one brown thin band on base, interior of aperture almost exclusively with dark brown band at cords. Spire moderately blunt, apex relatively blunt, tabulate, protoconch large, broad, whorl carination strong, shoulder and median cord almost equal in strength, large, distinct, slowly and subtly transitioning to clathrate sculpture, cords more spaced than in *P. pusilla*, scabrosity less evident than that species. First teleoconch whorl with P1, P2 spiral cords, second with P1, P2 cords, starting IP cord, third whorl with IP, P1, P2 cords, fourth with IP, P1, P2, P3, P4, P5, ADP, MP spiral cords, final whorl with 15 narrow, moderately spaced axial ribs. Aperture elongate ovate, moderately small, parietal and columellar wall extremely thin, canal rarely fused. Apertural denticle morphology somewhat weak, consisting of D1–D5.

Type Material: Holotype LACM 3764, length 7.5 mm, width 5.8 mm; paratype LACM 3766, length 5.4 mm, width 3.0 mm (Jade Cove, Monterey County, California (35°54'46" N, 121°28'29" W), on rocks at 14.6 m.

Type Locality: China Rock, Seventeen Mile Drive, Monterey County, California, (36°36'10" N, 121°57'42" W) on intertidal rocks.

Other Material Examined: Three specimens, in beach drift, Makah Bay, Clallam County, Washington, collected by Tom Rice [LACM 182327]; one specimen, Anchor Bay, Mendocino County, California, collected by D. Brown, July 1958 [LACM 61635]; one specimen, intertidal, Waddell Beach, Santa Cruz County, California (37°06'00" N, 122°19'59" W), collected by Hulda McLean, 1967–1968 [LACM 1967–95.60]; eight specimens at 18 m, Isle of St. James, North Farallon Islands, California (37°45'40" N, 123°05'57" W), collected by R.W. Schmieder, R/V CORDELL EXPLORER, 14 September 1991 [LACM 1991–177.23]; 23 specimens, intertidal on rocks, Carmel Point, Monterey County, California (36°31'00" N, 121°57'0" W), collected by J.H. McLean, 13–15 October 1981 [LACM 1981–47.25]; three specimens at 12.1–38.1 m, Carmel Submarine Canyon, north end San Jose Creek Beach, Monterey County, California (36°31'59" N, 121°55'59" W), collected by J.H. McLean, 1960–1964 [LACM 1960–24.106]; two specimens, intertidal on shale ledges and boulder reef, 0.4 km northwest of South Point, Shell Beach, San Luis Obispo County, California (35°09'18" N, 120°40'29" W), collected by P. I. LaFollette, 10 December 1977 [LACM 77–111.45]; one specimen, intertidal to 7.6 m, 0.48 km southeast of Bay Point, San Miguel Island, California Channel Ids., California (34°01'59" N, 120°17'59" W), collected by J.H. McLean, 21–22 August 1967 [LACM 1967–38.57]; one specimen, intertidal, Forney Cove, Santa Cruz Island, California Channel Ids., California (34°03'29" N, 119°55'00" W), collected by J.H. McLean, 15 March 1969 [LACM 1969–11.37]; two specimens at 23–27 m, on granite pinnacles, Wilson Rock, San Miguel Island, California Channel Ids., California (34°06'24" N, 120°23'41" W), collected by J.H. McLean, 31 May 1982 [LACM

1982–59.33]; 20 specimens at 9.1–30.4 m, Isthmus Cove, Santa Catalina Island, California Channel Ids., California (33°26'30" N, 118°28'59" W), collected by J.H. McLean, June–July 1971 [LACM 71–99.33]; six specimens at 9.1–21.3 m, Santa Barbara Island, California Channel Ids., California (33°28'59" N, 119°1'30" W), collected by J.H. McLean and J. Margetts, 8 July 1972 [LACM 72–97.38]; 13 specimens, San Pedro, Los Angeles County, California, collected by R.H. Tremper [LACM 59613]; five specimens, Laguna Beach, Orange County, California [LACM 17420]; two specimens from Reef Point, Orange County, California [LACM 17431]; three specimens, intertidal, south side of Punta Banda, Baja California, Mexico (31°43'36" N, 116°43'00" W), collected by J.H. McLean, 30 November 1963 [LACM 63–55.31]; 20 specimens at 15.2–30.4 m, Ben Rock, near Isla San Martin, Baja California, Mexico (30°25'59" N, 116°07'00" W), collected by J.H. McLean, 23 September 1972 [LACM 72–112.37]; five specimens at 13.7 m, northwest end of Isla Cedros, Baja California, Mexico (28°21'00" N, 115°14'48" W), collected by J.H. McLean, 24 September 1972 [LACM 72–114.36]; one specimen, intertidal, Punta Rompiente, Baja California, Mexico (27°43'22" N, 115°00'06" W), collected by J.H. McLean and P. I. LaFollette, R/V SEARCHER, 21 October 1971 [LACM 71–162.43].

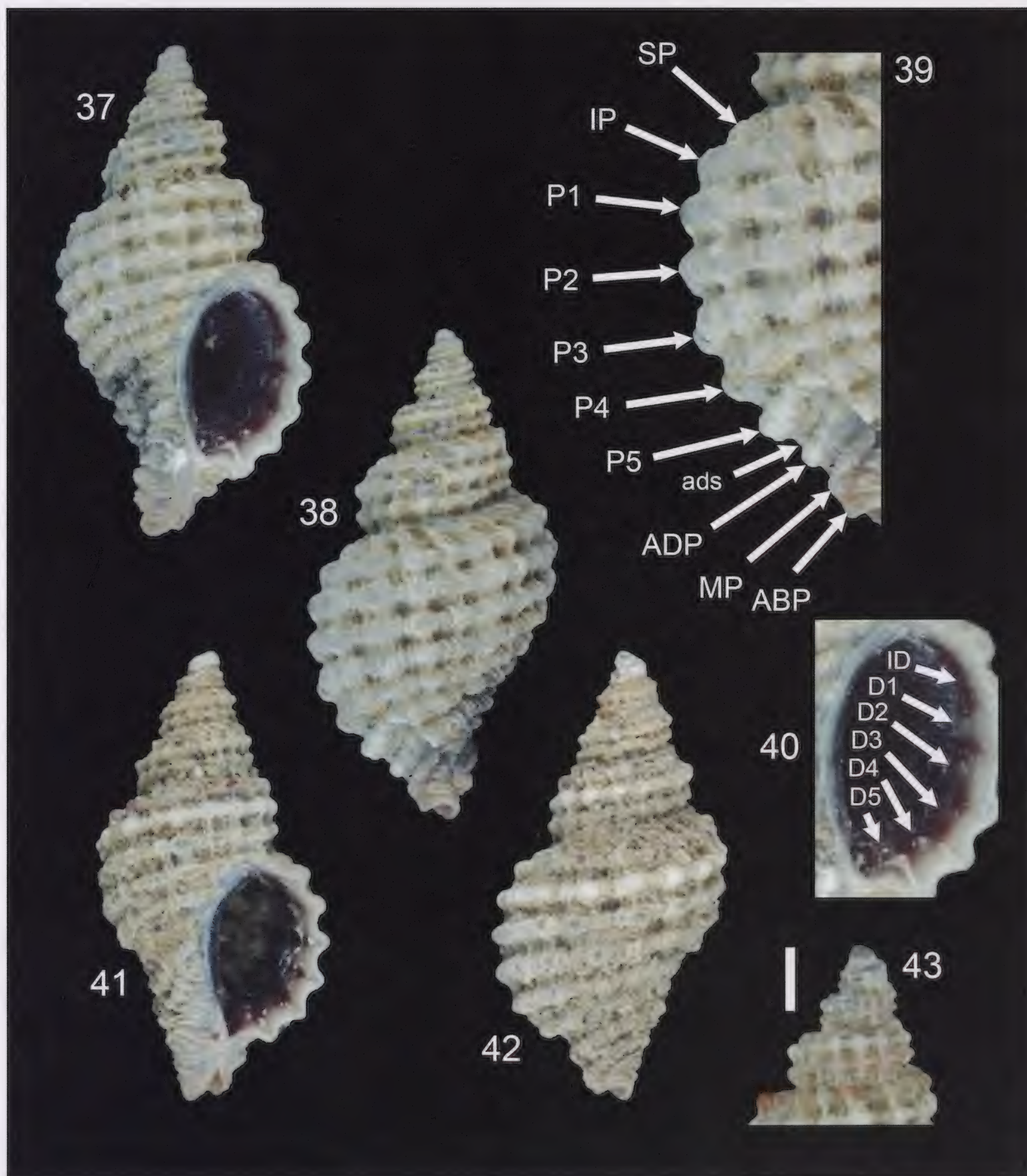
Distribution: Makah Bay, Clallam Co., Washington (48° N) to Punta Rompiente, Baja California Sur, Mexico (27° N); intertidal and subtidal zone on rocks to 125 m.

Remarks: The initial three teleoconch whorls are similar to *Paciocinebrina gracillima* (Stearns, 1871) (Figures 48–51), but *P. pseudopusilla* is absent of secondary cords. The general morphology is most similar to *P. pusilla*, protoconch features, spiral and denticle morphology (Figures 28–29, 39–40) are distinguishable characters in separating these species, considering additional characteristics is problematic and usually lend to improper identification. Protoconch of *P. pusilla* small, bulbous, highly erect, keel indistinct, *P. pseudopusilla* protoconch large, profile wide, tabulate, keel distinct, D6 cord present in *P. pusilla*, exclusively absent in *P. pseudopusilla*. Superficially similar to *P. pusilla*, initial two whorls identical, third whorl with P3 cord present in *P. pusilla*, absent in *P. pseudopusilla*, fourth whorl of *P. pusilla* with P6, s6 and ABP cords, D6 apertural denticle, and one fewer axial rib, characters not seen in *P. pseudopusilla*.

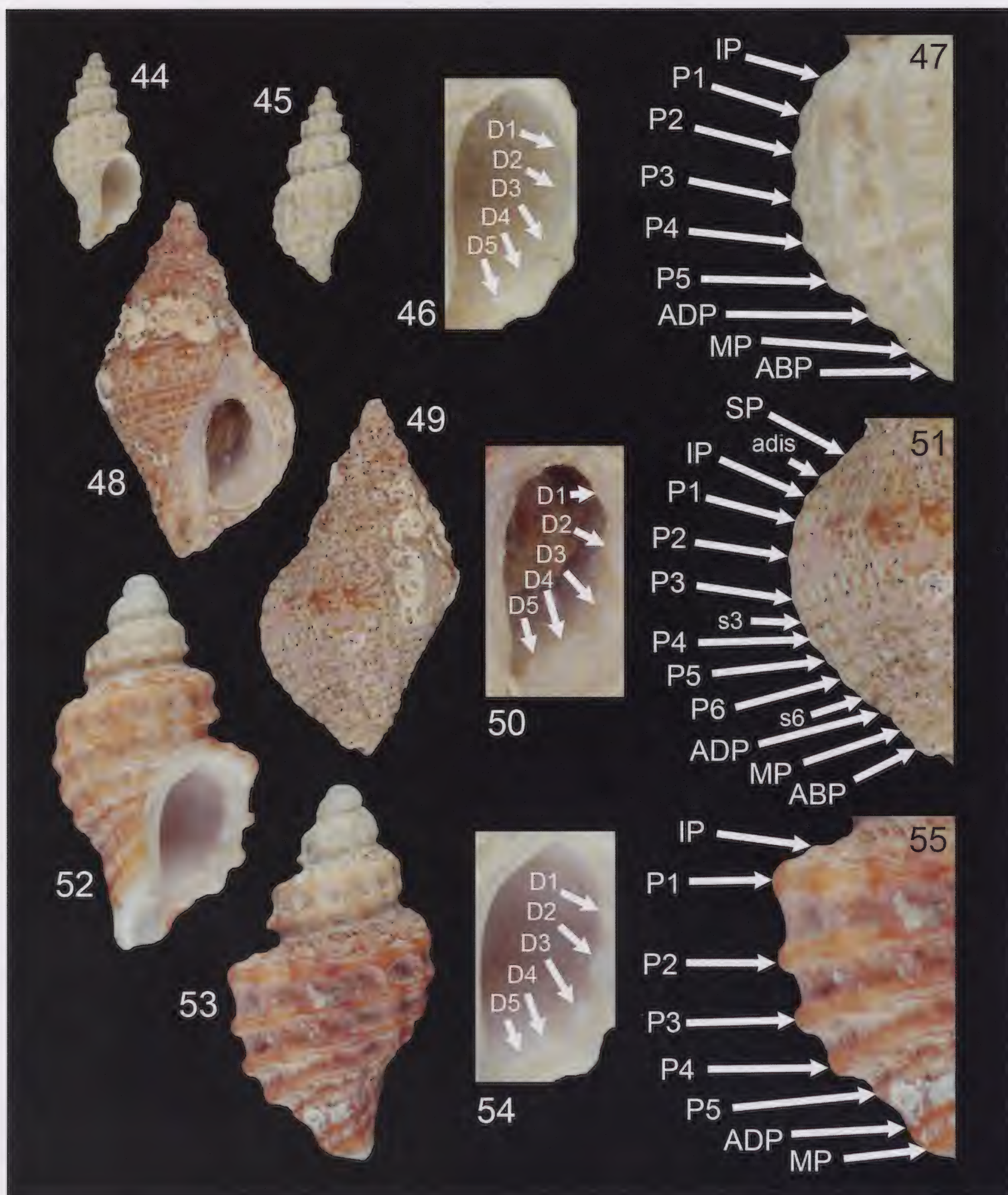
Etymology: Gender feminine, *pseudo*- meaning spurious and *pusilla* in reference to that morphologically similar species in the nominative case.

Paciocinebrina pusilla new species (Figures 37–43)

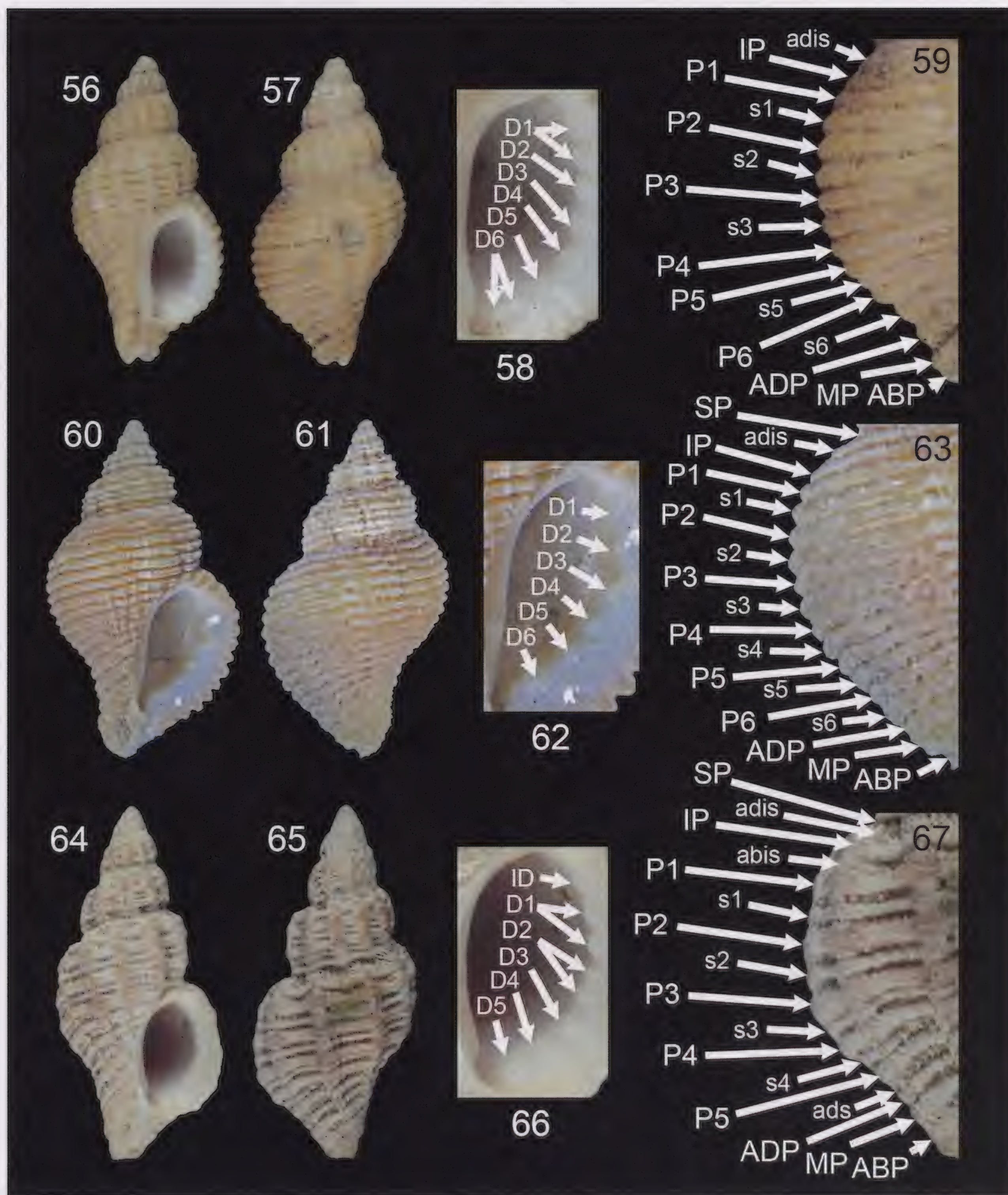
Description: Shell small for genus, holotype length 9.6 mm, width 5.2 mm. Shell elongate, rhomboid, sculpture clathrate, ribs somewhat tight, spiral cords thick, interspaces small, condensed, color white to dingy, gray brown, rarely with sienna brown blotches on IP cord, P1 cord often white, occasionally P3 cord with faint brown marks, interior of aperture dark purplish brown or white.



Figures 37–43. *Paciocinebrina pusilla* new species. 37–38. Holotype, Point Estero, California, on intertidal rocks, length 9.6 mm, width 5.2 mm (LACM 3765). 39. Spiral cords morphology. 40. Apertural denticles morphology. 41–42. Paratype, Cayucos, California, on intertidal rocks, length 8.8 mm, width 4.9 mm (LACM 3767). 43. Protoconch, scale bar: 1.0 mm (SGW 123).



Figures 44–55. *Paciocinebrina* species. **44–47.** *Paciocinebrina minor* (Dall, 1919). **44–45.** Holotype, Santa Catalina Island, California, length 7.3 mm, width 3.7 mm (USNM 56912). **46.** Apertural denticles morphology. **47.** Spiral cords morphology. **48–51.** *Paciocinebrina gracillima* (Stearns, 1871). **48–49.** Syntype, at 18.2 m, San Diego, California, length 13.4 mm, width 7.4 mm (USNM 46920). **50.** Apertural denticles morphology. **51.** Spiral cords morphology. **52–55.** *Paciocinebrina atropurpurea* (Carpenter, 1865). **52–53.** Lectotype, Neah Bay, Washington, length 14.0 mm, width 7.6 mm (USNM 15528b). **54.** Apertural denticles morphology. **55.** Spiral cords morphology.



Figures 56–67. *Paciocinebrina* species. **56–59.** *Paciocinebrina munda* (Carpenter, 1864). **56–57.** Holotype, Santa Catalina Island, California, length 16.4 mm, width 8.3 mm (USNM 46708). **58.** Apertural denticles morphology. **59.** Spiral cords morphology. **60–63.** *Paciocinebrina lurida* (Middendorff, 1848). **60–61.** Syntype, Sitka, Alaska, length 18.0 mm, width 10.5 mm (ZISP 62131). **62.** Apertural denticles morphology. **63.** Spiral cords morphology. **64–67.** *Paciocinebrina interfossa* (Carpenter, 1864). **64–65.** Holotype, Monterey, California, length 18.8 mm, width 9.3 mm (USNM 4636). **66.** Apertural denticles morphology. **67.** Spiral cords morphology.

Spire acute, protoconch small, relatively erect, initially projecting upward, bulbous, keel weak, shoulder and median cord almost equal in strength, intersected immediately by clathrate sculpture transitioning to pustulated intersections with evenly-spaced ribs, scabrocity highly prominent on subsutural ramp, between cords and on siphonal canal. First two teleoconch whorls with IP, P1, P2 spiral cords, third with IP, P1, P2 cords, starting SP cord, fourth whorl with IP, P1, P2, P3, P4, P5, P6, s6, ADP, MP, ABP cords, 16 narrow, but tightly spaced axial ribs on final whorl. Aperture elongate ovate, moderately large, somewhat restricted, parietal and columellar wall extremely thin, canal almost exclusively fused. Denticle morphology absent or very weak, only detectable in fully matured specimens, D1–D6 denticles thereafter.

Type Material: Holotype LACM 3765, length 9.6 mm, width 5.2 mm; one paratype LACM 3767 (Cayucos, San Luis Obispo County, California (35°26'50" N, 120°55'14" W), on intertidal rocks).

Type Locality: Point Estero, San Luis Obispo County, California (35°27'34" N, 120°58'15" N), on intertidal rocks.

Other Material Examined: One specimen, intertidal on rocks, Carmel Point, Monterey County, California (36°31'0" N, 121°57'0" W), collected by J.H. McLean, 13–15 October 1981 [LACM 81–47.26]; four specimens, Pacific Grove, Monterey County, California, collected by A. G. Smith, 1910 [LACM 182324]; two specimens, Monterey, Monterey County, California, Falkenthal collection [LACM 182323]; three specimens, Monterey, Monterey County, California [LACM 182325]; five specimens, Monterey, Monterey County, California, collected by Howard Hill [LACM 182326]; one specimen, siftings from *Phyllospadix* roots, Hopkins Marine Station, Pacific Grove, Monterey County, California (36°37'30" N, 121°54'00" W), collected by J.H. McLean, 1 December 1962 [LACM 62–16.20]; one specimen, intertidal, Dinosaur Cave, Shell Beach, San Luis Obispo County, California (35°09'01" N, 120°40'36" W), collected by P.M. Oringer, 19 December 1968 [LACM 68–48.24]; two specimens, intertidal, near El Cortez Hotel, north of Ensenada, Baja California, Mexico (31°52'30" N, 116°40'48" W), collected by J.H. McLean and P.M. Oringer, 19 December 1964 [LACM 64–32.40]; one specimen, intertidal on rock ledges and boulders, 1.6 km south of Puerto Santo Tomás, Baja California, Mexico (31°34'59" N, 116°40'00" W), collected by J.H. McLean and P.M. Oringer, 4 January 1966 [LACM 66–1.47]; six specimens, intertidal, cement plant halfway between village and beach at Puerto Santo Tomás, Baja California, Mexico (31°33'00" N, 116°40'00" W), collected by J.H. McLean, 8–10 January 1967 [LACM 67–2.58].

Distribution: Carmel Point, Monterey Co. California (36° N) to south of Puerto Santo Tomás, Baja California, Mexico (31° N); chiefly intertidal on rocks. This species seems to inhabit cold waters to the north and reappears in the cold upwelling regions of northern Baja California.

Remarks: The first whorl with visible IP, P1 and P2 cords which is identical to other *Paciocinebrina* species, second whorl identical to *P. lurida* and *P. interfossa*, fourth and final whorl of *P. pusilla* lacking secondary cords not present in the other two species. See *P. pseudopusilla* section for comparisons of this similar species. This species is commonly confused as juvenile specimens of *Paciocinebrina atropurpurea* and *P. interfossa*.

Etymology: Gender feminine, *pusilla* meaning little in the nominative case.

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A new species of *Arca* (Bivalvia: Arcidae) from the lower Miocene Asahi Formation on the Japan Sea side of central Honshu, with remarks on the westward faunal migration from the eastern Pacific

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ABSTRACT

The arcid bivalve, *Arca* (*Arca*) ***budoensis* new species**, is described from the Budo Mudstone Member of the Asahi Formation in northern Niigata Prefecture, central Honshu. The age of the member has been assigned to 16.6–15.9 Ma (late early Miocene) on the basis of dinoflagellate cysts. Judging from the arcid, dinoflagellate cysts and sedimentary facies, the paleo-environment of the member was a shallow embayment influenced by a warm-water current. The reason that the molluscan fauna of the Budo Member contains no characteristic species of the subtropical to tropical Arcid-Potamid fauna (17.0–16.7 Ma) is that the Budo fauna is slightly later than that Arcid-Potamid fauna. Because the new species resembles fossil and Recent species of the eastern Pacific, *A. budoensis* is accepted as derived from an ancestor that migrated westward to Asia. **The senior author, Kazutaka Amano, is the single author of the new species.**

Additional Keywords: Marine, fossil, shallow sea, warm-current

INTRODUCTION

The Japan Sea was formed in the latest Oligocene (ca. 25 Ma) by separation of the Japanese Islands from the Eurasian continent (Yanai et al., 2010). The oldest “marine” trace fossils from the Japan Sea side were recovered from the Shiose-no-Misaki sediments which were intruded by a dolerite dated at 20 Ma (Ohguchi et al., 2005). However, Sato et al. (2009) argued that these fossils were non-marine. According to Sato et al. (1991, 2009), the oldest marine fossils including the nannofossil, *Sphenolithus heteromorphus* were from the lower part of the NN4 zone (Martini, 1971), later than 17.75 Ma according to Backman et al. (2012).

In the northern part of Niigata Prefecture, the marine sediments occur in the Miocene Asahi Formation (Nishida, 1958; Takahama et al., 1976), which unconformably overlies the Tenjosan Formation and is overlain by the Osudo Shale containing the Osudo flora (Kamoi et al., 1978). This flora corresponds with the late early to early Middle Miocene Daijima-type flora (Takahama

et al., 1976; Kamoi et al., 1978). The Asahi Formation consists of the Budo Mudstone, Nagasakatoge Rhyolite and Arasawa Sandstone and Conglomerate Members in ascending order (Takahama et al., 1976). The large foraminifer *Operculina complanata japonica* Hanzawa, from the Arasawa Member indicates a late early to early late Miocene age (Kamoi et al., 1978).

The following mollusks and brachiopods (including *Terebratulina* spp.) were recorded from the Budo Member by Nishida (1958), Tsuda (1965) and Takahama et al. (1976): *Chlamys iwasakiensis*, *Pecten* sp., *Cardium* sp., *Geloina yamanei*, *Panomys simotomensis*, and *Littolinopsis miodelicatula*. Of these, *Geloina yamanei* and *Littolinopsis miodelicatula* are characteristic species of late early Miocene mangrove swamp fauna (Oyama, 1950). However, these species names were only listed up from unknown localities and have never been described nor illustrated. Moreover, the exact age of this member has not been determined from microfossils.

Many marine fossils have been recovered from a previously unknown locality in the Budo Member. The species composition including a new arcid species is very different from the above listed species. In this paper, we determine the age by dinoflagellate cysts, describe the new bivalve species of *Arca* and discuss the paleobiological significance of the fauna.

MATERIALS AND METHODS

The fossils were collected from a small outcrop along a rice field at 250m east from Budo (Figure 1; 38°23'23" N, 139°33'27" E). At the fossil locality, hard gray mudstones yielding many shell-dissolved fossils are exposed. From this locality, the following molluscan species are recorded: ***Arca budoensis* new species**, *Arcuatula*? sp. and *Cavilucina*? sp. Moreover, the fossils also include three species of brachiopods: *Discinisca* sp., *Coptothyris grayi* (Davidson), *Terebratalia* sp. and one fragment of *Cirripedia*, *Capitulum*? sp.

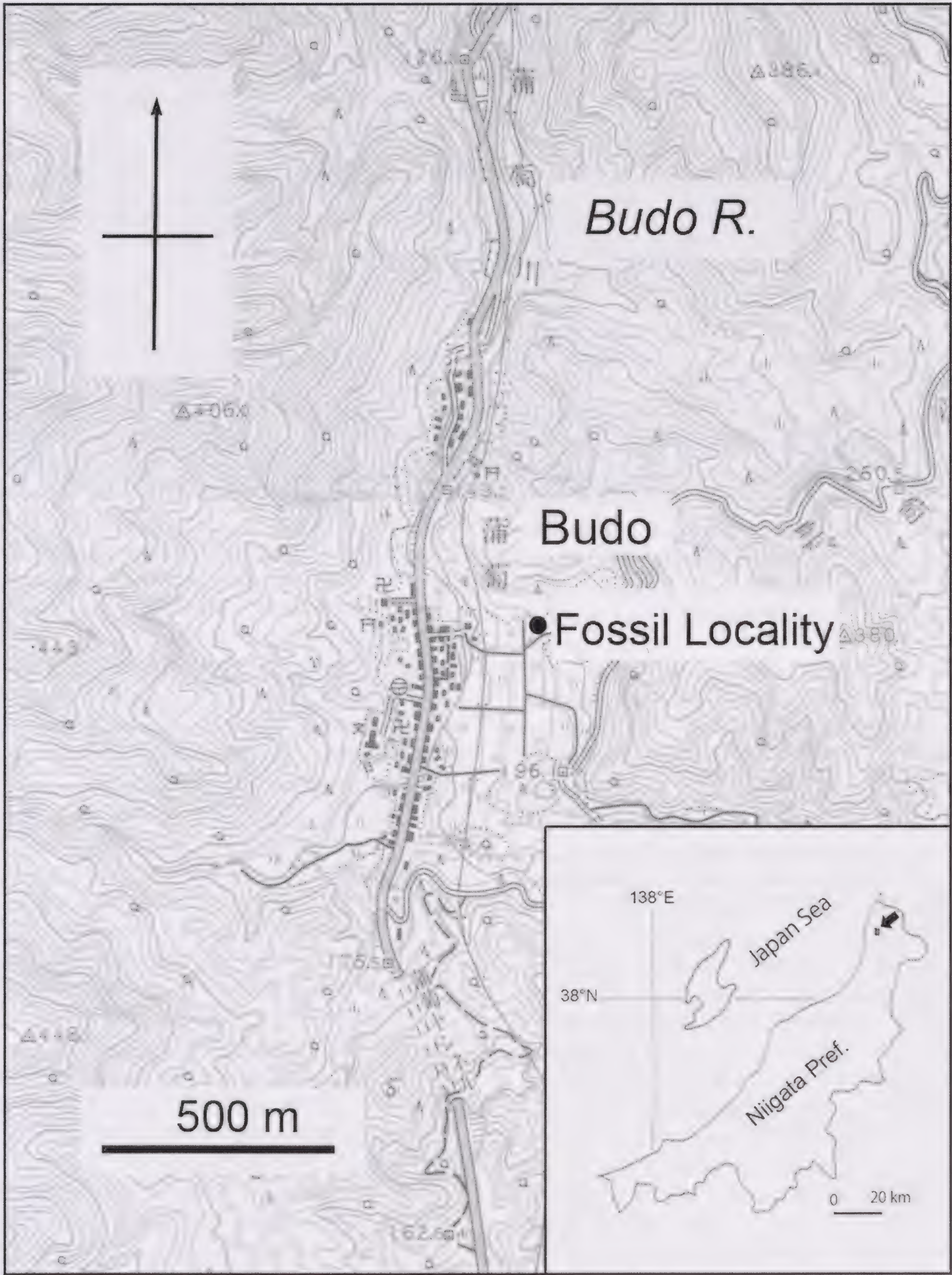


Figure 1. Locality of fossils. Base map from “Budo”, original scale 1:25,000; topographical map published by the Geospacial Information Authority of Japan.

Dinoflagellate cysts were picked for age determination from the rock subsampled in the mollusk-bearing mudstone. Taxonomic identification of dinoflagellate cysts follows Fensome et al. (2008), where complete bibliographic references were provided. The sample was treated successively with HCl and HF to eliminate carbonate and silicate minerals. Then heavy liquid zinc bromide (specific gravity 2.0) was used to concentrate organic particles from the residues after the acid treatment.

We used digital calipers (Mitsutoyo Company, model CD-20) to measure specimens of *Arca* to the first decimal

place. The terminology on *Arca* is follows Noda (1966). All specimens of *Arca* are deposited at the National Museum of Nature and Science, Tsukuba (NMNS).

DINOFLAGELLATE AGE

The sample yielded a number of dinoflagellate cysts whose preservation was sufficiently good for identification. Based on 393 counted specimens, the dinoflagellate cyst assemblage is characterized by abundant to common

occurrences of *Achomosphaera ramulifera*, *A. spongiosa*, *Cribroperidinium giuseppeii*, *C. granomembraneceum*, *Diphyes latiusculum*, *Heteraulacacysta campanula*, *Hystriochokolpoma rigaudiae*, *Lingulodinium machaerophorum*, *Operculodinium centrocarpum*, *Spiniferites pseudofurcatus* and *Systematophora placacantha* with fewer *Nematosphaeropsis lemniscata*, *Reticulatosphaera actinocoronata*, and *Tuberculodinium vancampoeae*. In the assemblage, protoperidinioid species are very minor in abundance and include *Brigantedinium* sp., *Lejeunecysta* spp., and *Selenopemphix nephroides* (Table 1). In addition, a few specimens of an acritarch species *Paralecaniella indentata* and a freshwater green alga *Pediastrum* sp. were also recorded.

The abundant to common occurrences of *Cribroperidinium giuseppeii*, *C. granomembraneceum*, *Diphyes latiusculum*, *Spiniferites pseudofurcatus* and *Systematophora placacantha* indicate evident correlation with the basal part of the Subzone b of *Diphyes latiusculum* Zone originally proposed by Matsuoka et al. (1987) and subsequently modified by Obuse and Kurita (1999). According to Obuse and Kurita (1999), this part is coeval

Table 1. List of dinoflagellate cysts and acritarchs associated with the molluscan fossils. Relative abundance of each dinoflagellate cyst taxon is expressed as VA (very abundant, 20 % and more of the total specimen count), A (abundant, 20–10 %), C (common, 10–3 %), R (rare, 3–1 %) and VR (very rare, less than 1 %).

Species	Abundance
DINOFLAGELLATA	
<i>Achomosphaera ramulifera</i>	C
<i>Achomosphaera spongiosa</i>	C
cf. <i>Achomosphaera spongiosa</i>	R
<i>Batiacasphaera</i> ? spp.	VR
<i>Brigantedinium</i> sp.	VR
<i>Cleistosphaeridium ancyrea</i>	VR
<i>Cribroperidinium giuseppeii</i>	C
<i>Cribroperidinium granomembraneceum</i>	C
<i>Diphyes latiusculum</i>	C
<i>Heteraulacacysta campanula</i>	R
<i>Hystriochokolpoma rigaudiae</i>	R
<i>Impagidinium</i> sp.	VR
<i>Lejeunecysta</i> spp.	VR
<i>Lingulodinium machaerophorum</i>	C
<i>Lingulodinium</i> sp.	VR
<i>Nematosphaeropsis lemniscata</i>	VR
<i>Operculodinium centrocarpum</i>	C
<i>Reticulatosphaera actinocoronata</i>	VR
<i>Selenopemphix nephroides</i>	VR
<i>Spiniferites membraneceus</i>	R
<i>Spiniferites pseudofurcatus</i>	C
<i>Spiniferites ramosus</i>	R
<i>Spiniferites</i> sp.	A
<i>Systematophora placacantha</i>	VA
<i>Tuberculodinium vancampoeae</i>	R
Other organic algal microfossils	
<i>Paralecaniella indentata</i>	present
<i>Pediastrum</i> sp.	present

with the diatom *Denticulopsis praelauta* Zone (NPD3B) that is calibrated to the age interval of 16.6–15.9 Ma (latest early Miocene) by Yanagisawa and Akiba (1998) and Watanabe and Yanagisawa (2005).

SYSTEMATICS

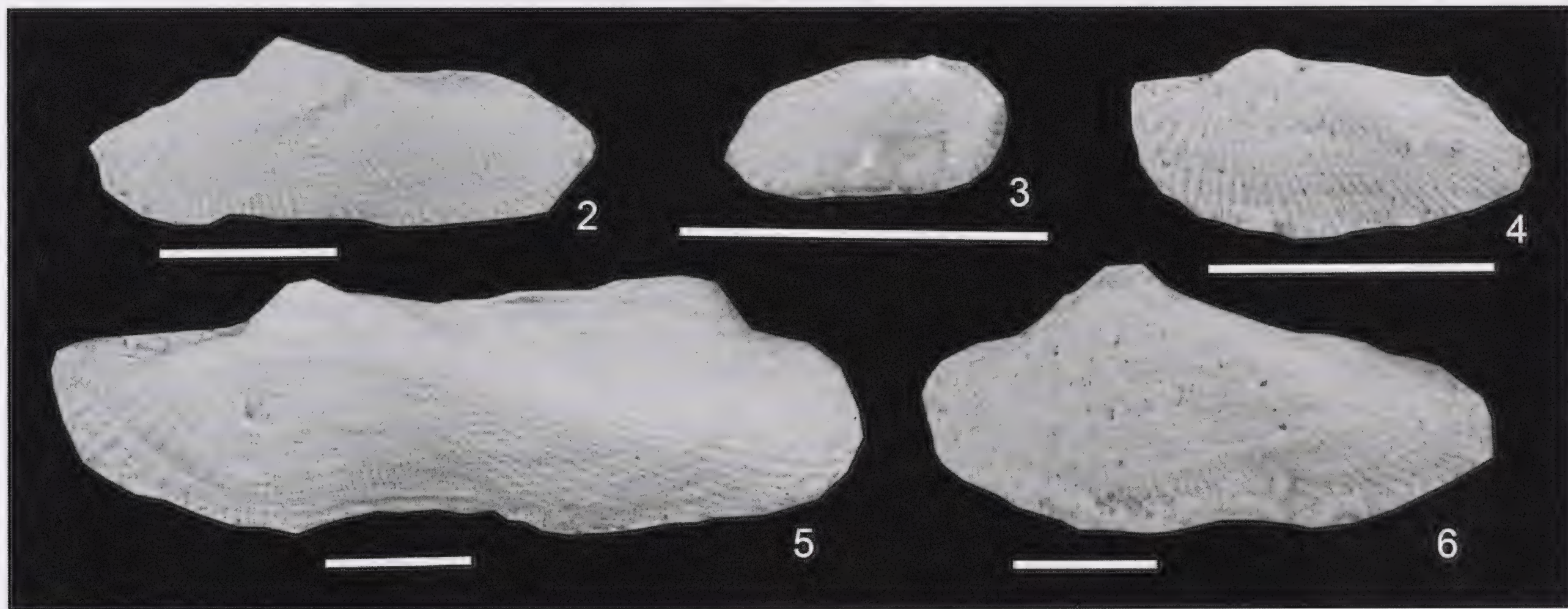
Family Arcidae Lamarck, 1809
Subfamily Arcinae Lamarck, 1809
Genus *Arca* Linnaeus, 1758
Subgenus *Arca* Linnaeus, 1758

Type Species: *Arca noae* Linnaeus, 1758 by subsequent designation.

Remarks: The senior author, Kazutaka Amano, is the single author of the new species. Reinhart (1935) recognized four subgenera: *Arca*, *Litharca* Gray, 1842, *Arcoptera* Heilprin, 1887, and *Eonavicula* Arkell, 1929. According to Lutaenko and Maestrati (2007), *Litharca* is an independent genus and *Arcoptera* is independent from *Arca* (s.s.). Oliver and Chesney (1994) recognized *Tetrarca* Nordsieck, 1969 (type species: *Arca tetragona* Poli, 1795). When Oliver and Holmes (2006) subdivided *Arca* into *A. noae*, *A. avellana*, and *A. tetragona* groups, they did not treat the last group as a separate subgenus. Consequently, Lutaenko and Maestrati (2007) separated the extinct *Arcoptera* as a subgenus and *Arca* (s. s.) into three types: Type 1 (*A. avellana*, *A. boucardi*, *A. tetragona*), Type 2 (*A. navicularis*, *A. pacifica*, *A. zebra*) and Type 3 (*A. koumaci*), based on the presence of postero-dorsal wing and posterior sulcus. Huber (2010) subdivided the modern *Arca* into four subgenera as *Arca* (s. s.), *Tetrarca*, unnamed I (*A. avellana*, *A. imbricata*, *A. mutabilis*, *A. ventricosa*) and unnamed II (*A. boucardi*). From the view point of valve margins, Vermeij (2013) subdivided *Arca* into three groups as *A. imbricata* group with smooth edge (*A. avellana*, *A. imbricata*, *A. mutabilis*), *A. zebra* group with obsolete ventral crenulations and well-developed anterior and posterior ones (*A. zebra*, *A. pacifica*, *A. navicularis*, *A. ventricosa*, *A. noae*). Vermeij (2013) separated *A. boucardi* from these two groups by its continuously crenulated ventral margin and a much narrower hinge plate. Molecular data by Feng et al. (2015) and Kong et al. (2020) support the subdivision of *Arca* (s. s.) by Oliver and Holmes (2006) and Lutaenko and Maestrati (2007) except for the separation of *A. boucardi* as a subgenus level supporting Huber’s (2010) and Vermeij’s (2013) opinions. In this paper, the new species is treated as a *A. noae* group (Subgenus *Arca* s. s.) from its shell shape.

***Arca (Arca) budoensis* Amano new species**
(Figures 2–6)

Diagnosis: Small *Arca* having low elongate shell, pointed anterior end, truncated posterior margin, strong radial ridge from umbo to postero-ventral corner and posterior sulcus. Surface ornamented with 64 radial ribs and granulated with growth lines on posterior part.



Figures 2—6. *Arca (Arca) budoensis* Amano new species. **2. Paratype**, left valve, NMNS PM 65048. **3. Paratype**, right valve, NMNS PM 65050. **4. Paratype**, left valve, NMNS PM 65049. **5. Holotype**, left valve, NMNS PM 65046. **6. Paratype**, left valve, NMNS PM 65047. Scale bars = 5 mm.

Description: Shell small (to 25.8 mm long), elongate quadrate, much lower than high especially in adults ($H/L = 0.33$ to 0.56), inequilateral ($AL/L = 0.27$ to 0.41), strong radial ridge extending from umbo to postero-ventral corner. Antero-dorsal margin straight and horizontal; anterior end of dorsal margin pointed; antero-ventral margin posteriorly oblique; middle to posterior ventral margin broadly concave as byssal notch in adult but straight in younger specimens (length < 7.3 mm); postero-ventral corner acutely rounded; posterior margin subtruncated and concave; postero-dorsal margin straight and horizontal making right angle with posterior margin. Umbo produced above dorsal margin; beak located at anterior about one-third to two-fifths. Surface of anterior part of shell in front of radial ridge ornamented with 51 flat and fine radial ribs separated by nearly equal interspaces; anterior eight stronger than other ribs; posterior area of shell behind radial ridge sculptured by 13 radial ribs, lamellated growth ribs making granules at their crossing points; granulation sometimes seen in front of radial ridge in younger shells. Small taxodont teeth observable in terminal of hinge. Inner structure unknown.

Type Material: Holotype: Left valve (NMNS PM no. 65046), length 25.8 mm, height 8.6 mm, anterior length 7.6 mm. Paratypes: Left valve (NMNS PM no. 65047), length 19.6 mm, height 7.7 mm, anterior length 8.0 mm; left valve (NMNS PM nos. 65048), length 13.8 mm, height, 5.0 mm+; left valve (NMNS PM no. 65049), length 7.3 mm, height 4.1 mm, anterior length 2.9 mm; right valve (NMNS PM no. 65050), length 3.7 mm, height 1.9 mm, anterior length 1.0 mm.

Type Locality: 250m east from Budo, Murakami City; upper lower Miocene Budo Mudstone Member of Asahi Formation.

Material Examined: Twenty-eight specimens from the type locality.

Remarks: From the point of view of shell shape, there is no similar modern or fossil species in Japan. *Arca* sp. from the uppermost lower Miocene Kubohara Formation in Gifu Prefecture by Itoigawa et al. (1981, 1982) has a similar shell size and an elongate shell. However, *Arca (Arca) budoensis* new species has a pointed anterior end and lower shell than *Arca* sp.

Arca (Arca) budoensis new species can be included in the *A. noae* group of Oliver and Holmes (2006) and Type 2 by Lutaenko and Maestrati (2007) because of its wing shape and posterior sulcus. In the western Pacific, there is no fossil record other than the modern species, *Arca (Arca) navicularis* Bruguière, 1789 belonging to the same group and type. However, the oldest record of *A. (A.) navicularis* is from the Pliocene in Indonesia (Kase et al., 2008). *Arca (Arca) budoensis* new species differs from *A. (A.) navicularis* by having a lower shell, no pointed postero-dorsal end and finer radial ribs. In contrast, some similar species have been described from the eastern Pacific. *Arca (Arca)* cf. *hawleyi* Reinhart, 1943 from the Eocene Tejon Formation in California, is similar to the new species by having a similar size elongated shell with a pointed anterior end and a strong ridge from beak to postero-ventral corner. However, *Arca (Arca) budoensis* new species has a more posteriorly situated beak and more distinct radial ribs. A Recent species, *Arca (Arca) pacifica* (Sowerby, 1833) from Baja California to the Galápagos Islands (Coan and Valentich-Scott, 2012) is similar to the new species in having pointed anterior end and a concave area behind the strong ridge from beak to postero-ventral margin. However, *Arca (Arca) budoensis* new species has a lower elongate-quadrate shell, no pointed posterior end, shallower byssal notch and more numerous fine radial ribs and is much smaller than *A. (Arca) pacifica*. Another similar species is *Arca (Arca) truncata* (Sowerby, 1833) from San Lucas, Baja California

to the Galápagos Islands (Coan and Valentich-Scott, 2012). It resembles *Arca (Arca) budoensis* new species in its low elongate quadrate outline. *Arca (Arca) budoensis* new species has a pointed antero-dorsal end, a posterior sulcus and an oblique posterior margin which are never observed in the much larger *A. (A.) truncata*.

Distribution: Only from the type locality.

Etymology: Named for locality from where this species was collected.

DISCUSSION

The present paper is the first to describe and illustrate fossils from the Budo Member. *Arca (Arca) budoensis* new species and its associated species indicate a shallow-marine environment. The occurrences of the dinoflagellate cysts *Lingulodinium machaerophorum* (cold-intolerant/thermophilic) and *Tuberculodinium vancampoe* (tropical to subtropical) suggest the influence of a warm current (Head, 1997; de Vernal and Marret, 2007). Moreover, the occurrence of a freshwater alga *Pediastrum* sp. suggests proximity to a river that fed the embayment. This inference was also supported by the sedimentary facies analysis (Igarashi and Kurita, 2007). The shallow-marine molluscan fauna herein described is different from the tropical to subtropical Arcid-Potamid fauna (Tsuda, 1965), despite them sharing a similar paleoenvironment. Recently Yanagisawa and Watanabe (2017) postulated that the occurrence of the Arcid-Potamid fauna in Japan was confined to the interval of 17.0 to 16.7 Ma. As the Budo Member was deposited slightly later (16.6 to 15.9 Ma) than the Arcid-Potamid fauna, it does not include any characteristic species of the fauna. However, most species of Type 2 and the *Arca noae* group to which *Arca (Arca) budoensis* new species belongs live in warm water which is concordant with the paleoenvironment inferred by the dinoflagellate cysts.

As described here, *Arca (Arca) budoensis* new species resembles both fossil and modern species from the eastern Pacific, not from the western Pacific. In the early Miocene, six bivalve genera and one subgenus have been recognized as immigrants from the eastern Pacific to the west during the early to early middle Miocene. The taxa include the venerids *Securella*, *Kaneharaia*, *Compso-myax*, the hiattellid *Panomys*, the rock-boring myid *Platyodon*, the Pholadid *Penitella*, and the tellinid subgenus *Rexithaerus* (Amano, 2005). One modern species of the Type 2 (Lutaenko and Maestrati, 2007) in the western Pacific, *Arca (Arca) navicularis* first appeared only in the Pliocene of Java, Indonesia (Kase et al., 2008). Thus, *Arca (Arca) budoensis* new species was derived from the ancestor which migrated from the eastern Pacific to Japan at least by the early Miocene.

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RESEARCH NOTE

Imposex in the city: First evidence of female masculinization in Queen Conch *Aliger gigas* (Linnaeus, 1758) (Gastropoda: Strombidae) in Florida

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Organotins, such as tributyltin (TBT), are chemical compounds added to antifouling paint that were used worldwide on oceangoing vessels from the 1960s until 2008, when the International Maritime Organization banned them globally through the International Convention on the Control of Harmful Antifouling Systems on Ships (Horiguchi, 2017; Laranjeiro et al., 2018). The use of organotins adversely impacted growth, development, and reproduction in numerous marine organisms (Horiguchi, 2017; Vogt et al., 2018). Despite the global ban, organotins can persist in the environment for decades (Filipkowska et al., 2014; Horiguchi, 2017), thus still posing a threat to susceptible species. In gastropods, organotin exposure can lead to the development of a condition known as imposex (Bryan et al., 1988; Horiguchi, 2017). Imposex is the superimposition of male reproductive tissues (i.e., penis and vas deferens) onto female gastropods and is caused by disruption of the neuroendocrine system (Oberdorster et al., 2005; Horiguchi, 2017). Continued exposure to organotins increases masculinization in females and can reduce fecundity (Averbuj and Penchaszadeh, 2010). In severe cases, the vaginal opening is blocked, resulting in sterility (Bryan et al., 1988; Horiguchi et al., 1995), ultimately leading to large population declines (Cadee et al., 1995; Horiguchi et al., 2006). Imposex in the natural environment is almost exclusively associated with organotin exposure (Oehlmann et al., 2007; Sternberg et al., 2010; Horiguchi, 2017), to the point that imposex in gastropods is used as a biomarker for TBT contamination (Oehlmann et al., 2007; Horiguchi, 2017).

The incidence of gastropod imposex is higher near shipping channels, industrial seaports, and marinas (Li and Collin 2009; Averbuj and Penchaszadeh, 2010; Laranjeiro et al., 2018). The Queen Conch, *Aliger gigas* (Linnaeus, 1758), is a large, gonochoristic marine gastropod that has been protected in Florida since 1986 because of overfishing. A well-documented breeding aggregation of Queen Conch (Berry et al., 2016) sits adjacent to Port Everglades (Figure 1), one of the busiest industrial seaports in the United States (<http://www.porteverglades.net>). And while TBT-induced imposex in areas of elevated boating activity occur in the Caribbean (Titley-O'Neal et al., 2011), imposex has never been reported in Queen Conch in Florida.

We conducted a demographic survey of the Port Everglades Queen Conch aggregation on August 30, 2007, and another on June 27, 2018. A 100-m tape was deployed along one margin of the aggregation; five secondary tapes were then placed perpendicular to the primary tape at random intervals. A secondary tape extended either 100 m into the aggregation or, if positioned at a point at which the aggregation was less than 100 m wide, to its distant margin. Scuba divers counted all adult Queen Conch (defined as having a fully flared lip approximately 10 mm thick or more) within 1 m either side of the secondary tapes to estimate the density of the aggregation. Identifying the sex of a conch *in situ* requires turning it over and patiently waiting for its body to emerge. Because of the time constraints of scuba surveys, individuals were not sexed, but reproductive behaviors (i.e., mating and egg laying) were noted.

Our two aggregation surveys yielded comparable results in terms of density and the percentage of Queen Conch engaged in reproductive behaviors. In 2007, we surveyed 1000 m² and counted 73 adult Queen Conch, for a density of 730 ha⁻¹. Of these, 5.5% were mating and 9.6% were laying egg masses. During the 2018 survey, we surveyed 850 m² and counted 42 adult Queen Conch, for a density of 494 ha⁻¹. Of these, 4.8% were mating and 11.9% were laying egg masses.

During the 2018 survey, nine female conchs (so identified because they were mating or egg laying) were collected for assessment of ovarian condition. After removing the bodies from their shells, we observed and recorded that some of these females exhibited imposex (Figure 2). We moved on to collect a sample of ovary tissue from each female, excising a piece of tissue approximately 1 cm³ from the middle of each ovary. The samples were placed in labeled plastic cassettes and fixed for seven days in 10% neutral buffered formalin. Following fixation, we prepared the ovarian tissues for histological assessment of ovarian maturity and the percentage of developed ovarian tissue using the methods of Delgado et al. (2004). For each female, we also recorded

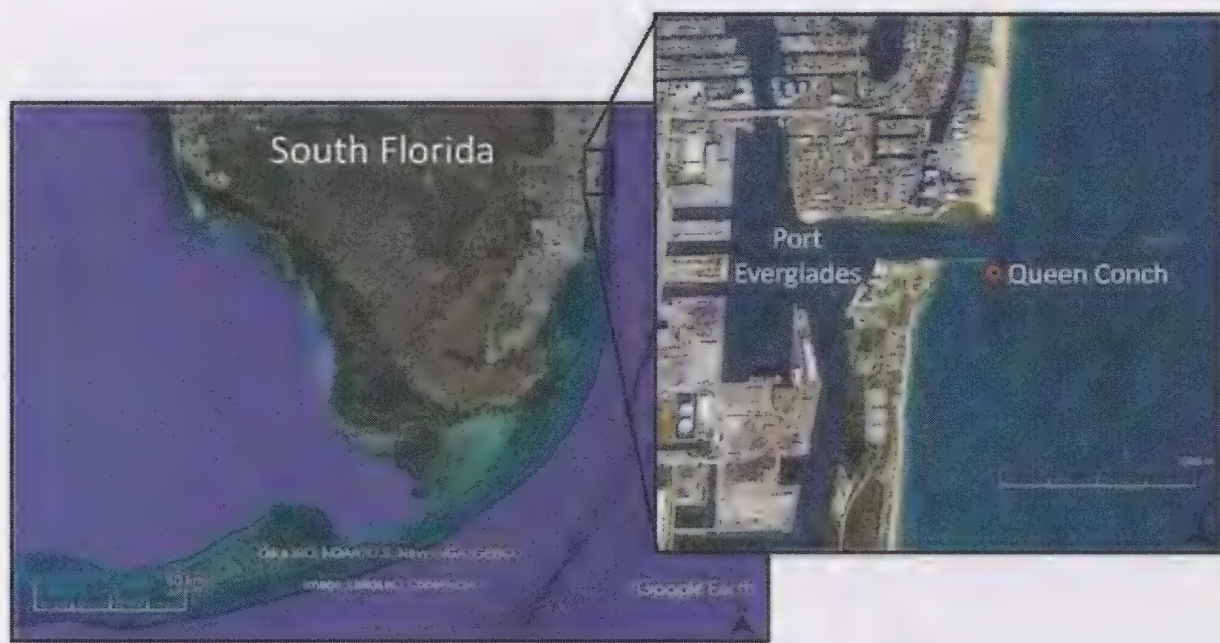


Figure 1. Map of South Florida indicating the location of Port Everglades. Inset shows the site of the Queen Conch aggregation found at the entrance to Port Everglades.

four morphological measurements, as described by Delgado et al. (2019): shell length, lip thickness, shell weight, and body weight. Unpaired t-tests, performed in Sigma Plot 13 (Systat Software Inc., San Jose, CA, USA), were used to test for differences in histology and morphology between females exhibiting imposex and normal females. Results were considered statistically significant if $P < 0.05$.

For each female, we ranked the severity of imposex using the scale developed by Cob et al. (2011), which ranges from 0 (i.e., normal; no imposex) to 3 (i.e., having a complete penis). Imposex was observed in four of the nine females (44.4%). One female was characterized as having stage-1 imposex (Figure 2). The other three females were characterized as having stage-2 imposex (Figure 2). From histology, all four females with imposex were classified as ripe and spawning-capable (i.e., they had tertiary vitellogenic oocytes, with oocytes in the oviduct; Figure 3). Imposex-affected and normal females did not differ significantly in shell length ($t = -1.514$; $df = 7$; $P = 0.174$),

lip thickness ($t = 0.037$; $df = 7$; $P = 0.972$), shell weight ($t = 1.275$; $df = 7$; $P = 0.243$), body weight ($t = -1.976$; $df = 7$; $P = 0.089$), or the percentage of developed ovarian tissue ($t = 1.331$; $df = 7$; $P = 0.225$) (Table 1).

This is the first documented case of imposex in Queen Conch in Florida. While we did not test for the presence of organotins at the aggregation site, the proximity to a major shipping port suggests that organotin exposure was the likely cause of the malady (Oehlmann et al., 2007; Sternberg et al., 2010; Horiguchi, 2017). The marine habitats surrounding Port Everglades are almost certainly contaminated with organotins that predate the antifoulant ban in 2008 as evident by the fact that the nearby disposal site for dredged material from Port Everglades is heavily contaminated by organotins (U.S. EPA and USACE 2020). Although organotin is banned from being sold in 67 countries, it is still manufactured and sold in many Caribbean and South American countries (Turner and Glegg, 2014). Ships originating from these countries may be a more recent source of contamination.

There may be other endocrine disruptors that might be causing imposex at Port Everglades, but the overwhelming evidence from the literature suggests organotin exposure (Oehlmann et al., 2007; Sternberg et al., 2010; Horiguchi, 2017). That said, the extent of organotin contamination around South Florida is unknown. Future research should include water, sediment, and tissue assays to determine the extent of organotin contamination around South Florida and could also include a local member of the widespread *Stramonita haemastoma* (Linnaeus, 1767) species complex such as *Stramonita floridana* (Conrad, 1837) to serve as a bioindicator (*sensu* Stickle and Zhang, 2003; Limaverde et al., 2007).

In contrast to studies finding that imposex negatively affects reproduction in gastropods (Horiguchi et al., 2006; Lahbib et al., 2009; Averbuj and Penchaszadeh, 2010),



Figures 2. Two imposex-affected female Queen Conch from Port Everglades, Florida (removed from shells).

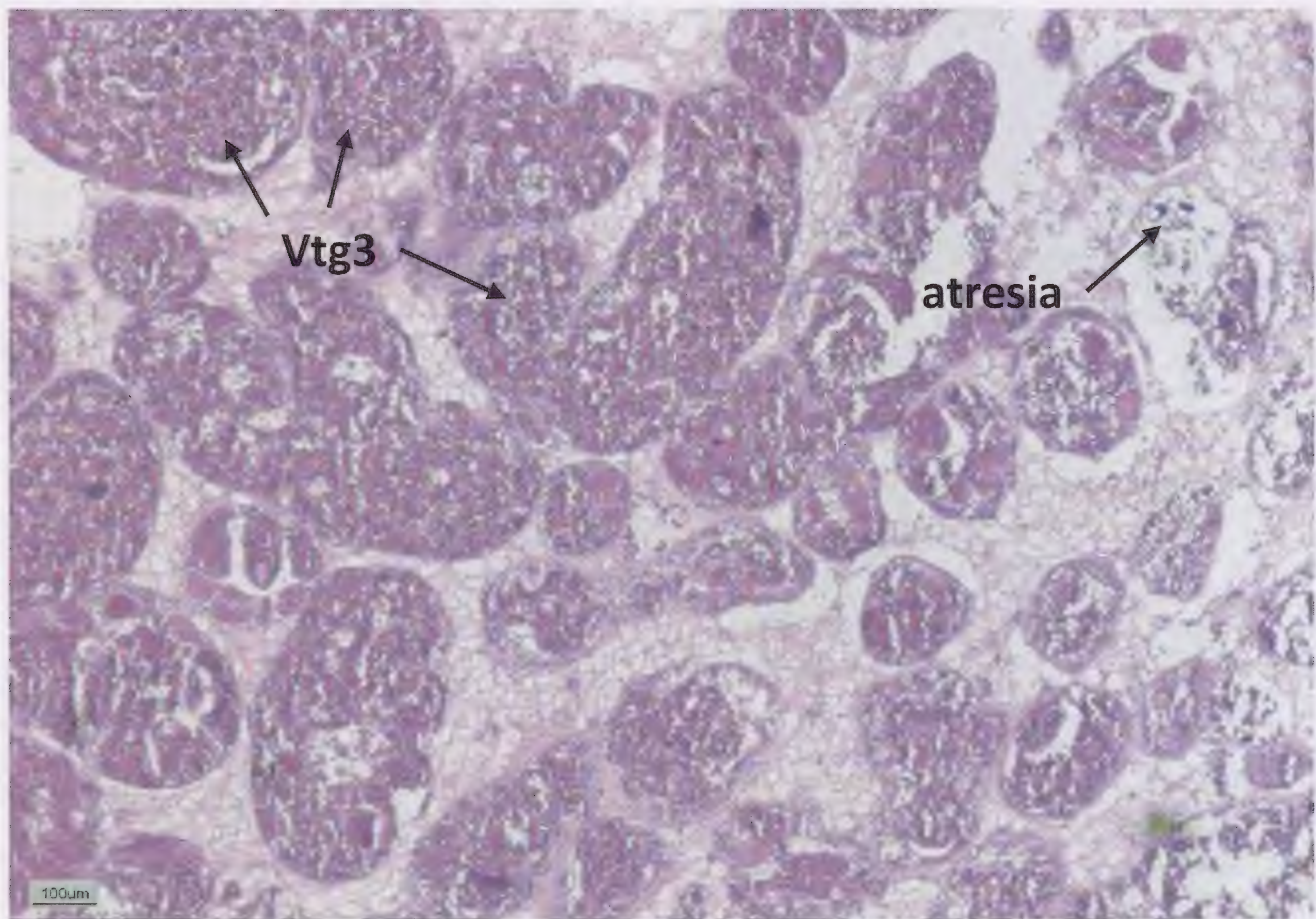


Figure 3. Histological section of ovarian tissue from an imposex-affected Queen Conch from Port Everglades, Florida. This female was classified as ripe and spawning-capable. Note the abundant tertiary vitellogenic oocytes (Vtg3) throughout the ovarian tissue; minor atresia (i.e., resorption of some vitellogenic oocytes) can also be seen.

the >40% incidence rate of imposex in our samples did not seem to affect reproductive activities. The percentage of Queen Conch mating and laying eggs in the Port Everglades aggregation was similar to that reported elsewhere in Florida (Delgado and Glazer, 2020), where no imposex has been reported (Delgado et al., 2004, 2019). Based on histology, the ovaries of the females afflicted with imposex were indistinguishable from those of normal, ripe females. This may be because, while the incidence rate of imposex was relatively high, the severity of the affliction was not in the advanced stages. The

Table 1. Morphological and histological measurements (mean \pm 1 standard error) of female Queen Conch from Port Everglades, Florida.

	Imposex-affected	Normal
Shell length (cm)	22.5 \pm 0.62	23.8 \pm 0.58
Lip thickness (mm)	28.3 \pm 2.01	28.2 \pm 1.32
Shell weight (g)	2,615 \pm 161	2,338 \pm 146
Body weight (g)	355 \pm 29.6	474 \pm 47.9
Ovarian tissue (%)	97.0 \pm 1.92	92.8 \pm 2.35

females we examined were engaged in reproductive activities, which may have biased our results; there may be females within the aggregation with more severe cases of imposex that are not reproductively active. Future research might explore the relationship between age and imposex severity and incidence rate, because older females will have been exposed longer.

Studies of imposex in other strombids have reported morphological differences between imposex-affected and normal females. In *Strombus pugilis* Linnaeus, 1758 and *Conomurex luhuanus* (Linnaeus, 1758), imposex-affected females were larger and heavier than normal females (Reed, 1993, 1995). In *Laevistrombus canarium* (Linnaeus, 1758), imposex-affected females had larger and heavier shells but lighter bodies than did normal females (Cob et al., 2008). However, we did not observe statistically significant differences in gross morphology between imposex-affected and normal females. This may have been because of the comparatively mild severity of imposex in the females we examined.

Imposex can cause population declines in gastropods (Cadee et al., 1995; Horiguchi et al., 2006), but this was not observed in Queen Conch at Port Everglades. The

demographics of the aggregation remained steady over our two surveys and were consistent with those reported by Berry et al. (2016). Berry et al. (2016), however, noted abnormal egg masses at the Port Everglades aggregation. Normal egg masses are crescent shaped and covered with sand; the abnormal ones were stringy and not covered with sand (Berry et al., 2016: fig 7). We also observed females laying abnormal egg masses. In other gastropods, egg laying becomes disrupted in advanced stages of imposex (Horiguchi, 2017), which may explain why some Queen Conch females at Port Everglades lay abnormal egg masses, but further study is needed.

It is unknown whether the offspring of imposex-affected females are as viable as those from normal Queen Conch. Other pollutants can cause transgenerational effects in mollusks that reduce larval growth and survival (Nice et al., 2003) and juvenile fitness (Osborne et al., 2020). If the veligers and juveniles from imposex-affected Queen Conch are compromised, this may have negative consequences for larval connectivity to downstream populations and metapopulation persistence.

Beyond the effects on Queen Conch, the results from this study highlight the deleterious impacts that society may have on wildlife resources that are juxtaposed closely to urban centers. Organotins represent only one in a much wider suite of chemicals that enter the South Florida nearshore marine environment from sources as diverse as agriculture (e.g., fertilizers, herbicides, pesticides), industry, recreation (e.g., golf course fertilization and pesticide application), and residential activities (e.g., sewage). How society values these resources and prioritizes the mitigation of the pernicious threats associated with point and non-point sources of pollution will ultimately determine the overall health of nearshore ecosystems and the sustainability of the resources they support.

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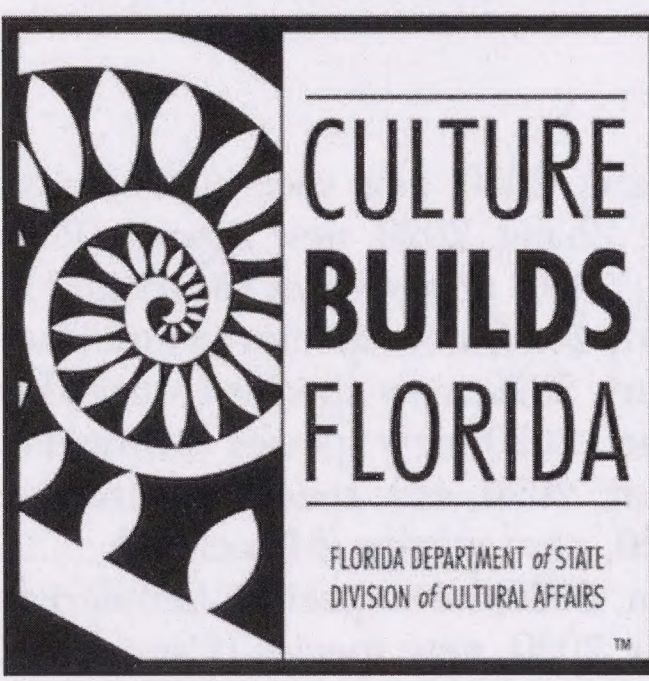
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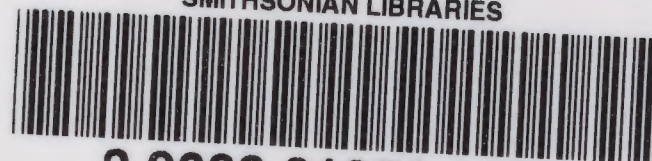
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